

EFFECT OF HUMIDITY UPON SURVIVAL AND DEVELOPMENT OF TERMITES

**Inaugural-Dissertation
zur Erlangung der Doktorwürde
am Fachbereich Biologie
der Freien Universität Berlin**

submitte by
Muhammad Ahmad Khan
Pakistan

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1. Referent: Prof. Dr. Dr. h. c. Günther Becker

2. Referent: Prof. Dr. Jürgen Brandenburg



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1. INTRODUCTION

Termites live in standing trees and dead wood, also in wooden structures, but mainly in the soil. They build different types of nests, as there are well known large mound of some soil-dwelling termites e.g. Macrotermitidae and arboreal nests of Nasutitermes and Microcerotermes species. Some species live only inside the wood without any outside visible nest structure, e.g. Kalotermes and Cryptotermes species or other dry-wood termites. In this way, termites live in a special microclimate which is relatively protected from surrounding atmospheric conditions. Of all the physical factors effecting the life of the termites, temperature and moisture are the most important ones. In the microclimate of the nests, the termites maintain their own high and more or less constant moisture conditions.

According to R. V. Fyfe and F. J. Gay (1938) relative humidity was 92 % inside the nest of Nasutitermes exitiosus in Australia. During the dry period in Tansania (Tanganyika) relative humidity inside the mounds of termites was higher than outside (R. Geigy, 1948). Similar results are shown by P. P. Grassé and C. Noirot (1948) and P. P. Grassé (1948), A. E. Emerson (1956) and M. Lüscher (1961).

Humidity is a most important physical factor for the distribution (O. L. Williams, 1934, A. E. Emerson, 1955, J. H. Calaby and F. J. Gay, 1959), nesting behaviour (C. Noirot, 1958/59), timing of swarming flights and postflight behaviour (P. Bodot, 1966, W. L. Nutting, 1966) and for the reproduction (P. Bodot, 1966) of the termites.

Termites depend on the high and more or less constant moisture conditions inside the nests as environmental condition. It has been stated by S. F. Cook and K. G. Scott (1932) that Zootermopsis angusticollis lost water rapidly when it was kept in dry air. If this loss of water is not compensated it may be fatal. At saturated atmospheric moisture, as in the microclimate

of the nest, termites showed the maximum survival period under starvation conditions. This has been stated among others by O. L. Williams (1934) with *Reticulitermes hesperus*, *Reticulitermes tibialis* and *Zootermopsis angusticollis*, by K. Gösswald (1941) with *Reticulitermes lucifugus*, by P. K. Sen-Sarma and P. N. Chatterjee (1966a) with *Microcerotermes besoni*, by E. Ernst and R. Geigy (1956) with *Kaloterms flavicollis*, *Zootermopsis angusticollis*, *Reticulitermes lucifugus* and *Nasutitermes arborum* and by Jan Krecek (1969) with *Heterotermes tenuis*, *Prorhinotermes simplex*, *Anoplotermes schwarzi*, *Nasutitermes rippertii* and *Nasutitermes costalis*.

The survival time of *Kaloterms flavicollis* under starvation conditions in relation to the relative humidity has been investigated by G. Becker (1942, 1948), O. L. Williams (1934), K. Gösswald (1941), O. Klee (1960), P. K. Sen-Sarma (1965) and others. Dry-wood termites can withstand low atmospheric moisture. But the optimum relative humidity for the survival of *Kaloterms flavicollis* under starvation conditions is a little below 100 %. Similarly maximum survival of *Cryptotermes brevis* was observed at 87 % relative humidity (D. R. Minnick, S. H. Kerr and R. C. Wilkinson, 1973).

Kalotermitidae require less moisture than other species of termites (G. Becker, 1966b, 1969, M. S. Collins, 1969). They are more resistant against drying than Termopsidae, Rhinotermitidae and Termitidae (O. L. Williams, 1934, K. Gösswald, 1941, E. Ernst and R. Geigy, 1956, M. S. Collins, 1958, 1959 and R. M. C. Williams, 1976, 1977).

Of all the species of the genus *Reticulitermes*, *R. tibialis* is the most resistant to dryness (O. L. Williams, 1934, M. Strickland, 1950, M. S. Collins, 1963, 1969, G. Becker, 1970a).

The survival of termites under desiccation conditions differs not only in different species, but even in the same species from caste to caste (G. Becker, 1942, M. Strickland, 1950,

L. Dunmore and M. S. Collins, 1951, E. Ernst and R. Geigy, 1956, P. K. Sen-Sarma, 1969, 1974).

In a relative humidity gradient species of termites behaved differently according to their susceptibility against dryness. Termites which were sensitive to desiccation showed positive reaction faster than those species which were resistant to desiccation (K. Gösswald, 1941, E. Ernst and R. Geigy, 1956).

The intensity of the response to humidity fluctuations among termites is also influenced by the conditions of humidity to which they had previously been subjected. The groups of termites which were preconditioned in a dry atmosphere showed a quicker positive reaction in a relative humidity gradient than those groups which were kept in saturated air before the tests, e.g. *Microcerotermes beelsoni* (P. K. Sen-Sarma and P. N. Chatterjee, 1966b) and *Cryptotermes brevis* (D. R. Minnick, S. H. Kerr and R. C. Wilkinson, 1973).

Furthermore, the resistance against desiccation is also effected by group size. It has been stated among others by P. P. Grassé and R. Chauvin (1944), R. Geigy and E. Ernst (1956), G. Becker (1961a), G. Schultze-Dewitz (1962), P. K. Sen-Sarma (1965, 1969, 1974), M. S. Collins (1969), D. R. Minnick, S. H. Kerr and R. C. Wilkinson (1973) and P. K. Sen-Sarma and P. N. Chatterjee (1966a) that grouped termites are more resistant to dryness than isolated ones.

Termites have a special demand on the humidity of their feeding material wood. Dry-wood termites (*Kaloterms flavicollis*) prefer a lower wood moisture than other species of termites (G. Becker, 1965a and I. Hrdy, 1967).

Consumption of wood by the *Rhinotermitidae* species is not dependent on the moisture contents of the wood which is correlated with soil humidity, but on the water contents of the soil itself (G. Becker and D. Puchelt, 1961, G. Becker, 1962c, 1965a, 1970a). Moreover, wood deterioration did not depend on the type

of the soil (humus soil or sand), but on its water holding capacity (G. Becker, 1962c, 1965 a). The water holding capacity is low for pure sand and high for humus soil. In case of a substrate with a high water holding capacity, optimum conditions can occur in a rather broader range. This is a convenient fact for the maintenance during tests (G. Becker, 1965a).

In the attempt to find out useful methods to test the protection of wood against termites, the authors had used various substrates (sand, gypsum, humus soil and vermiculite) and various species of termites. Vermiculite was found to be the best substrate for the tests (G. Becker and M. Lenz, 1970, M. Lenz, G. Becker and M. Garcia, 1976). Species which showed high feeding quantity in relation to their body weights are very useful for the tests.

According to G. Becker (1948) the optimum moisture is very important for the development of different castes. Similarly, G. Becker (1969) stated that suitable moisture content of the substrate and the atmosphere are very important for the development of incipient colonies. G. Becker and M. Lenz (1970) carried out further examinations on the development of some species of termites. More work should be done in this direction.

If protection of materials from termites deterioration is wanted, one has first to examine the biology of these insects and the influence of environmental factors. One of the most important physical factors for the life of termites is moisture. Therefore, this examination was started.

The large number of termites species (more than 30 at the time), some of them with cultures from different geographical origin, cultured in the B. A. M. Berlin-Dahlem provided the opportunity of the investigation of many species.

In these investigations 19 species of termites were tested on survival, development and feeding activities in relation to moisture. These results are carried out in order to give a new knowledge about testing, maintenance and rearing methods of termites and also to give a better understanding of the occurrence of termites in nature.

2. MATERIAL AND METHODS

2.1. Origin ¹⁾ and geographical distribution of the tested species

The species of termites investigated belong to the following four families of the order Isoptera:

- | | |
|-----------------------------|-------------------------|
| 1. Kalotermitidae Enderlein | lower termites, |
| 2. Termopsidae Karny | symbiotic protozoa |
| 3. Rhinotermitidae Light | present in hindgut |
| 4. Termitidae Westwood | higher termites without |
| | symbiotic protozoa |

1. Family Kalotermitidae Enderlein (dry-wood termites)

The worker caste is absent in this group of termites. The colonies are small in number and the work is done by the pseudergates. In all the species, insects live inside the galleries excavated in the wood for feeding purposes. The dry-wood termites of the family Kalotermitidae can be kept without soil and they are less sensitive to lower relative humidity as compared to other termites.

Genus *Neotermes* Holmgren

Neotermes Holmgren is an in the tropical and subtropical parts of the earth very widely distributed genus. It has a great economic importance as it is a pest of the woodworks of structures and agricultural crops. The presence of *Neotermes* in living and dead stems and branches of trees is also not uncommon.

The species *Neotermes jouteli* (Banks) is distributed in the coastal areas of Florida, Cuba, the Bahamas and both the east and west coasts of Mexico as well as Socorro islands (E. M.

1) For details of origin of the species see G. Becker and R. Mannesmann (1968) and G. Becker (1978).

Miller, 1948, S. F. Light, 1933 - 1935). The investigated termite, *Neotermes jouteli*, cultures at 26°C and 90 % relative humidity in Berlin-Dahlem, was originally collected in Cuba in 1966.

Genus *Kaloterмес* Hagen

Kaloterмес is a genus of dry-wood termites very large in number of species, which is widely distributed in the tropics and subtropics and has a great economic importance in these parts of the world.

Kaloterмес flavicollis (Fabricius) is found in the humid parts of the Mediterranean zone in Europe, e.g. the coasts of Portugal, Spain, southern France, Italy, the Balkan and Black Sea coast and in Asia Minor, south of Gaza; in North Africa, e.g. Alexandria (Egypt), Tripolis (Libya), Tunis (Tunisia) and along the coasts of Algeria and Morocco. Individuals are found not only in living and dead trees or shrubs but also in constructional timber.

The cultured *Kaloterмес flavicollis* was initially collected from the island of Ischia (Italy) in autumn 1953 and has been kept at 26°C and 90 % relative humidity in Berlin-Dahlem since 1953.

Genus *Cryptoterмес* Banks

The genus *Cryptoterмес* Banks has a great economic importance in the tropical and sub-tropical parts of the world. Its species destroy the wood of buildings, furnitures and fiber products. According to K. Krishna (1961) the place of origin of this genus is still obscure. It is widely spread in areas with relative high atmospheric moisture, such as coastal areas and islands. Nevertheless, members of this genus are also capable of living under relatively dry conditions.

Cryptoterмес dudleyi Banks is a very widely dispersed species, which is found in Africa, Asia, Australia, New Guinea, Central

America, the Caribbean area and South America; most of these records are introductions. In the oriental region, it occurs in India, East Bengal, Sri Lanka, Indonesia (Java, Sumatra and Borneo), Malaya and the Philippines. According to M. P. D. Pinto (1941), it occurs in Sri Lanka at altitudes up to about 5700 feet but it is most common below 200 feet. *Cryptotermes dudleyi* was collected in 1962 in Mombasa/Kenya and has been cultured in Berlin-Dahlem at 30°C and 98/99 % relative humidity since that time.

2. Family Termopsidae Karny (damp-wood termites)

Some species belonging to this family have very small colonies and there is no worker caste, however the work is done by the pseudoworkers.

Genus *Zootermopsis* Emerson

Zootermopsis Emerson which is found in North America has attained a great importance for laboratory tests. Two very closely related species of *Zootermopsis*, *Zootermopsis angusticollis* (Hagen) and *Zootermopsis nevadensis* (Hagen), are distributed along the pacific coast of North America from Vancouver to the Mexican border.

Zootermopsis angusticollis is dominant in the coastal areas and it requires a relatively high moisture. These insects are found not only in building timber but also in moist tree stumps and dead logs in forests. Individuals can be cultured in small groups which readily develop neotenic reproductives. According to G. Becker (1967) *Zootermopsis angusticollis* prefers a low and narrow range of temperature (18 - 22°C). Investigations were carried out with *Zootermopsis angusticollis* (Hagen) collected at San Juan island and in Pudget Sound near Seattle (Wash., USA). The insects have been cultured and bred at 20°C at the Bundesanstalt für Materialprüfung (BAM) in Berlin-Dahlem since 1957.

3. Family Rhinotermitidae Light (soil- and wood-dwelling termites)

Rhinotermitidae are small, wood-eating, subterranean termites. All the species of this family tunnel the earth and build galleries consisting primarily of soil (G. Becker and K. Seifert, 1962). The soldiers of the genus *Coptotermes* give off a drop of sticky fluid from the frontal gland when they are alarmed.

Species of the genus *Coptotermes* seldom or never produce neotenic reproductives (F. J. Gay et al., 1955, I. Hrdy, 1966, G. Becker, 1966a), whereas, the neotenic reproductives are easily developed in the *Heterotermes* and *Reticulitermes* species. Investigations were carried out with the following species of soil- and wood-dwelling termites.

Genus *Heterotermes* Froggatt

The genus *Heterotermes* is found all over the tropical parts of America, Asia and Australia, whereas, only a single species of *Heterotermes* has been found in the Ethiopian region.

Heterotermes indicola (Wasmann) is found in India, Bangladesh, Pakistan, Afghanistan and Nepal (G. Becker, 1975b). It has also been collected up to 2500 meters in the Himalayas. *Heterotermes indicola* is a serious pest of woodworks of structures as well as of living plants and agricultural crops, particularly of sugar cane and corn.

These insects which have a great economic importance, are very small in size. Ancestors of the investigated termite, *Heterotermes indicola*, were assembled from Kanpur (U. P. India) in 1957. They have been reared at 30°C and 98/99 % relative humidity and at 26°C and 90 % relative humidity in Berlin-Dahlem for twenty years.

Genus *Coptotermes* Wasmann

Coptotermes is a purely tropical genus. Due to introduction

it has become cosmopolitan by transportation in ships, because they can live and develop easily without soil (T. E. Snyder, 1957, L. G. E. Kalshoven, 1962). According to G. Becker (1953) species of this genus are not only restricted to areas near the coastal areas or moist rain forests but live also in the mountains with scanty of rain and continuous drought periods. E.g. *Coptotermes crassus* Snyder is also found in the Sierra de Chuacús and in the Sierra de las Minas in Guatemala. According to A. E. Emerson (1955) *Coptotermes* originated in the oriental region and has dispersed during the cretaceous period.

Coptotermes formosanus (Shiraki) has a wide distribution in Asia throughout Japan, Formosa and South China. It is at home in the sub-tropical climate but by introduction, it is also widely distributed in other tropical parts of the world. It occurs in Sri Lanka, Hawaii, the Pacific islands, the southern United States, South and East Africa. In Pakistan it has been collected from Karachi (coastal area) (M. S. Akhtar, 1974).

Coptotermes formosanus is an extremely destructive termite which attacks not only buildings, furniture and living trees but also most of the agricultural crops (sugar cane, corn etc.). Tests were done with animals, which were initially collected from Lake Charles, La., USA in 1974 and has been bred at 30°C and 98/99 % relative humidity in Berlin-Dahlem.

Coptotermes niger Snyder as an economic important species is found in Guatemala, British Honduras, Costa Rica, Panama and Columbia. Like *Coptotermes formosanus* it is also a very destructive termite. *Coptotermes niger* (tested species) was collected from British Honduras in 1964 and has been cultured at 30°C and 98/99 % relative humidity in Berlin-Dahlem.

Genus *Reticulitermes* Holmgren

Reticulitermes Holmgren is distributed in the northern tempe-

rate zone of Europe, North-America and Asia, except for a few species which are found in Central America, e.g. *Reticulitermes tibialis* in Mexico.

Reticulitermes flavipes (Kollar) is widely dispersed in the east of North-America from the U.S./Canadian border to Mexico and Guatemala. It seeks shelter not only in logs and stumps but also in poles and constructional timber. As an introduced termite it has been collected in Vienna/Austria (V. Kollar, 1837), Hamburg/Germany (H. Weidner, 1937, H. Schmidt, 1954), Mannheim/Germany (H. E. Wichmann, 1957), Hallein/Austria (A. Kurir, 1958), Ontario/Canada (F. A. Urquhart, 1953, 1954), Ottawa, Ont./Canada (C. G. MacNay, 1961).

Reticulitermes flavipes, collected from Hamburg/Germany in 1953, from Hallein/Austria in 1960 and from Charleston, S. C./USA in 1961 has been cultured and bred at 26°C and 90 % relative humidity in Berlin-Dahlem.

Reticulitermes hesperus Banks is widely distributed in North-America, especially along the pacific coast from Canada to the northern coast of California. The insects which have been cultured at 28°C and 95/98 % relative humidity in the BAM, Berlin-Dahlem were collected in Los Angeles, Calif./USA in 1971.

Reticulitermes lucifugus (Rossi) occurs throughout the Mediterranean regions of Europe, the Near East and North Africa. It is dispersed at southern part of the Atlantic coast in France. *Reticulitermes lucifugus* has been collected in a warm room (used for riping bananas) at Munich/Germany in 1966. As an introduced termite, it had lived there for short time and was destroyed after its discovery. *Reticulitermes lucifugus* supplied for the tests, was originally collected from Francavilla/Italy in 1961, from Munich/Germany in 1967 and from Favone, Corsica/France in 1967. It has been cultured and bred in Berlin-Dahlem at 26°C and 90 % relative humidity.

Reticulitermes santonensis Feytaud, which occurs along parts of the Atlantic coast of France, is a serious pest for constructional woodwork and living plants. The experiments were done with insects which were originally collected at La Rochelle and kept at 26°C and 90 % relative humidity in Berlin-Dahlem since 1958.

Reticulitermes speratus (Kolbe) *kyushuensis* Morimoto occurs as a very destructive termite in Southern Japan and Korea, where it destroys not only wooden structures and living plants but also the agricultural crops. Test termites of *Reticulitermes speratus kyushuensis* were originally collected in Seoul/Korea in 1967. It has been cultured at 28°C and 95/98 % relative humidity since its collection.

Reticulitermes speratus (Kolbe) *speratus* Morimoto is dispersed as a very destructive pest in Japan. The laboratory culture of this species originated from insects which were collected near Tokyo/Japan and have been cultured at 26°C and 90 % relative humidity in Berlin-Dahlem since 1967.

Reticulitermes virginicus (Banks) is distributed in the Nearctic region. In the west it extends to southern Illinois and Missouri, southward to the coastal areas of Florida and Texas. It was also collected in Philadelphia, Pennsylvania (T. E. Snyder, 1953, F. M. Weesner, 1965) and Long Island, New York (T. E. Snyder, 1959).

Animals of this species were collected at Janesville, USA in 1963 and have been reared at 28°C and 95/98 % relative humidity in Berlin-Dahlem.

Reticulitermes tibialis Banks is widely distributed in the Nearctic region. It occurs in the valleys and desert areas of California down to Mexico. It ranges from sea level to altitudes of at least 7500 feet in the Rocky Mountains in Colorado (F. M. Weesner, 1965) and to 8000 feet in Arizona (N. Banks and T. E. Snyder, 1920). *Reticulitermes tibialis* was collected

from San Antonio, Texas/USA in 1959 and has been kept at 26°C and 90 % relative humidity in Berlin-Dahlem since that time.

Genus *Prorhinotermes* Silvestri

Prorhinotermes Silvestri is a small genus which is widely spread on the coastal areas throughout the world. It lives mainly in dead parts of the trees.

Prorhinotermes simplex (Hagen) is dispersed in Florida, Cuba, Jamaica and Puerto Rico. *Prorhinotermes simplex*, cultured in the laboratory (Berlin-Dahlem) at 28°C and 95/98 % relative humidity, was initially collected from Cuba in 1967.

4. Family Termitidae Westwood (nest-building termites)

It is the largest family, consisting of 3/4 of the known species of termites. Many are wood-eating, mostly sub-terrestrial or mound builders, whereas some of them make arboreal nests. Fungal combs are found in the nests of some species of Termitidae, e.g. of the sub-family Macrotermitidae. Separation of different castes is very much pronounced as compared to lower termites. A very distinctive worker caste is always present in this family.

Tests were done with the following species of this family.

Genus *Microcerotermes* Silvestri

The genus *Microcerotermes* is very large in number of species and is widely spread throughout the tropical parts of the world.

The species *Microcerotermes crassus* Snyder which occurs in South-East Asia, was collected from Thailand in 1966 and has been cultured in the laboratory at 30°C and 98/99 % relative humidity in Berlin-Dahlem.

Microcerotermes championi Snyder as a very notorious pest of agricultural crops and woodworks of buildings is widely spread all over the Indian subcontinent. Ancestors of the tested ter-

mite, *M. championi*, were originally collected from India (Goa) in 1975. They have been cultured and bred at 28°C and 95/98 % relative humidity in Berlin-Dahlem.

Genus *Nasutitermes* Dudley

The genus *Nasutitermes* contains many species and is primarily tropical in its distribution. However, as an introduced smple it occurs in various geographical regions. This termite destroys constructional wood, living trees as well as agricultural crops.

The species *Nasutitermes nigriceps* (Haldeman) is widely distributed throughout the Neotropical region. Ancestors of the tested termites were originally collected in Esquintla, Guatemala, in 1967. They have been cultured and bred at 30°C and 98/99 % relative humidity since that time. The laboratory colony in Berlin-Dahlem consists of millions of individuals in its nest.

The most important data on all the investigated genera and species of termites are shown in table 1.

Table 1

Tested species of termites, their origin and culture temperature

Family	Genus	Species	Origin		Year	Cult. Temp.
			Country	Place		
Kalotermitidae	Neotermes	jouteli (Banks)	Cuba	-	1966	26°C
	Kaloterms	flavicollis (Fabricius)	Italy	Ischia	1953	26°C
	Cryptotermes	dudleyi Banks	Kenya	Mombasa	1962	30°C
Termopsidae	Zootermopsis	angusticollis (Hagen)	USA	Seattle, Wash.	1957	20°C
Rhinotermitidae	Heterotermes	indicola (Wasmann)	India	Kanpur	1957	30°C and 26°C
	Coptotermes	formosanus (Shiraki)	USA	Lake Charles La.	1974	30°C
	Coptotermes	niger Snyder	Brit. Honduras	-	1964	30°C
	Reticulitermes	flavipes (Kollar)	Germany	Hamburg	1952	26°C
	Reticulitermes	flavipes	Austria	Hallein	1960	26°C
	Reticulitermes	flavipes	USA	Charleston	1961	26°C
	Reticulitermes	hesperus Banks	USA	Los Angeles	1971	28°C
	Reticulitermes	lucifugus (Rossi)	France	Favone Corsica	1967	26°C
	Reticulitermes	lucifugus	Italy	Franca-villa	1961	26°C
	Reticulitermes	lucifugus	Germany	Munich	1967	26°C
	Reticulitermes	santonensis Feytaud	France	La Rochelle	1958	26°C
	Reticulitermes	speratus (Kolbe)	Korea	Seoul	1967	28°C
		kyushuensis Morimoto				

Family	Genus	Species	Origin		Year	Cult. Temp.
			Country	Place		
Termiti- dae	Reticuli- termes	speratus (Kolbe) speratus Morimoto	Japan	Tokyo	1967	26°C
	Reticuli- termes	tibialis Banks	USA	San An- tonio (Texas)	1959	26°C
	Reticuli- termes	virginicus (Banks)	USA	Janes- ville	1963	28°C
	Prorhino- termes	simplex (Hagen)	Cuba	-	1967	28°C
	Micro- cero- termes	championi Snyder	India	Goa	1975	28°C
	Micro- cero- termes	crassus Snyder	Thai- land	-	1966	30°C
	Nasuti- termes	nigriceps (Haldeman)	Guate- mala	Esquint- la	1967	30°C

2.2. Method for starving experiments

2.2.1. Control of relative humidity

Different percentages of relative humidity were controlled with super saturated solutions of inorganic salts (according to W. P. Winston and H. D. Bates, 1960). Relative atmospheric moisture was regulated in seven different stages with the following salts and distilled H_2O :

- | | | |
|---------------|---|-----------------|
| 1. $MgCl_2$ | super saturated solution in distilled H_2O | $\approx 33 \%$ |
| 2. NH_4NO_3 | " " " " " " | $\approx 63 \%$ |
| 3. $NaCl$ | " " " " " " | $\approx 75 \%$ |
| 4. KCl | " " " " " " | $\approx 85 \%$ |
| 5. Na_2SO_4 | " " " " " " | $\approx 93 \%$ |
| 6. K_2SO_4 | " " " " " " | $\approx 98 \%$ |
| 7. | 100 % relative humidity was controlled with pure distilled H_2O . | |

Each of the super saturated solutions of inorganic salt was kept in a glass vessel (100 mm ϕ x height 30 mm), and was then kept in a plastic box (180 mm x 180 mm x 60 mm) which was covered with a transparent lid. The lids of the plastic boxes were not quite airtight, a little exchange of air was possible for breathing of the insects. As the lids of the boxes were transparent the observations were possible without disturbing the termites.

The relative humidity which was checked regularly at each stage during the tests with Lambrecht's hair hygrometer, showed fluctuations of $\pm 2 \%$. The salt solutions were observed regularly and kept super saturated by adding distilled H_2O or salts during the experiment. It was important to avoid the deposition of salts at the walls of the glass vessels.

2.2.2. Handling of insects

The insects were taken out of the nest very gently and carefully to prevent them from infractions. They were counted with the help of a very fine tweezer to avoid injury of the insects during the handling. In order to protect the animals from desiccation during handling they were put on wet filter paper. After weighing, the insects were used for the tests as soon as possible. The size of test group and the caste to be tested differed with the various species of termites according to the availability of material from the cultures.

2.2.3. Selection of insects

The selection of the insects was done according to the following criteria: workers - maximum size, with full pigmentation; pseudo-workers - middle sized individuals in the colony; soldiers - maximum size, with full pigmentation of head and mandibles; and nymphs with well developed wingpads.

2.2.4. Containers

Depending upon the size and number of insects provided in each test group, two different sizes of containers were taken. Test groups of *Nasutitermes nigriceps*, *Coptotermes formosanus*, *Coptotermes niger* and *Zootermopsis angusticollis* were kept in small petri-dishes (50 mm ϕ x 20 mm). The lids of the petri-dishes were tight enough to avoid the escape of insects and were not airtight. Glass tubes (20 mm ϕ x 60 mm) were used as containers for the rest of the species of termites. The containers were kept in plastic boxes surrounding the glass vessels with salt solutions. The arrangement of apparatus for the tests is shown in fig. 1.

2.2.5. Inspections

During the first five days, the tests were controlled every

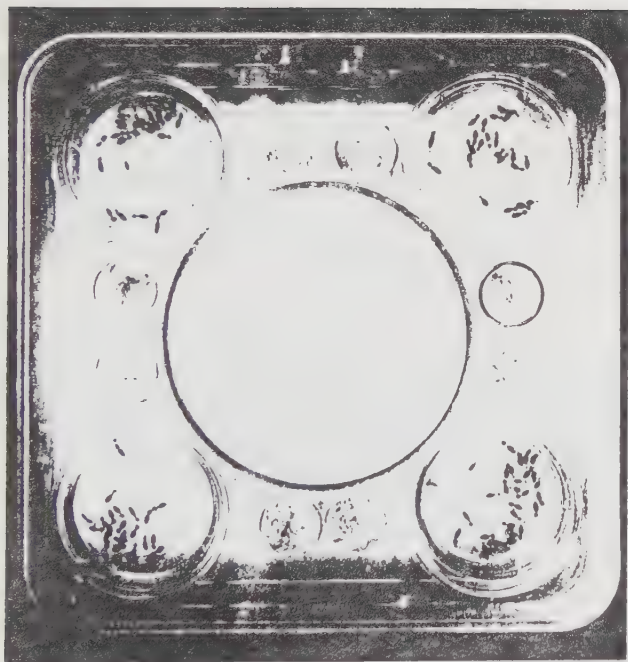


Fig. 1 - The arrangement of apparatus for starving experiments. This photo shows the plastic box covered with a lid, containing small petri dishes and glass tubes (with insects) and a glass vessel (in the middle) with super saturated salt solution (in surface view).

24 hours and in the following days every 48 hours. Above 75 % relative humidity the insects which had died within the first 24 hours were replaced by new individuals. Due to heavy condensation of water at 100 % relative humidity of the atmosphere it was necessary to change the containers at every observation to prevent the drowning of the insects. Dead animals were removed at each examination up to 100 % mortality. The dead bodies of the insects were examined carefully to observe whether cannibalism had occurred during the test. The number of the living as well as dead insects was counted in each test group to observe if any insect was missing due to cannibalism.

Average survival was calculated in days from total number of the insects taken at each stage of relative humidity in each species. All the species of termites were tested at 26°C except that of *Z. angusticollis* which was tested at 20°C because of its lower temperature preference.

2.3. Method for the feeding experiments

2.3.1. Containers

Two different sizes of transparent boxes of plastic material were used as containers for the various species of termites. For Rhinotermitidae, Kalotermitidae and Termopsidae species, small 307 cm³ boxes (6,5 cm x 4,5 cm x 10,5 cm) (Fig. 2) and for Termitidae species, cylindrical 572 cm³ boxes (9 cm ϕ x 9 cm) (Fig. 3) were supplied as containers. The lids of all boxes (containers) had very fine pores through which passage of air was possible for the breathing of the insects.

2.3.2. Substrate

For the experiments with *N. nigriceps* humus soil was taken as the substrate while vermiculite was used for all the other species. Vermiculite (product of C. H. E., Neuß/Rhein) is a mica material consisting of aluminium-iron-magnesium-silicate. Vermiculite and humus soil were dried at 100°C for six to seven hours and then sieved through a 1 mm pored sieve.

To each 307 cm³ box (container) 15 g vermiculite (3,5 cm layer) and 572 cm³ box (container) 25 g vermiculite (4,5 cm layer) was added. For the tests with *N. nigriceps* 150 g humus soil (3,5 cm layer) was filled in each 572 cm³ box (container).

2.3.3. Moisture content

K. flavicollis was tested with 50, 100, 200, 300, 350 and 400 % water contents in vermiculite while all the other species were tested in the same way but without 50 % water contents in vermiculite.

The humus soil used for the *N. nigriceps* tests had the following different water contents: 26, 30, 34, 38 and 42 %. The highest water holding capacity of humus soil was about 48 %. The water contents were calculated from the dry weight of the



Fig. 2 - Four-cornered 307 cm³ (4.5 cm x 6.5 cm x 10.5 cm) box used as a container for Kalotermitidae, Termopsidae and Rhinotermitidae species. This photo was taken of *Heterotermes indicola* after two weeks test period. The box contains 15 g vermiculite with a water content of 300 per cent.

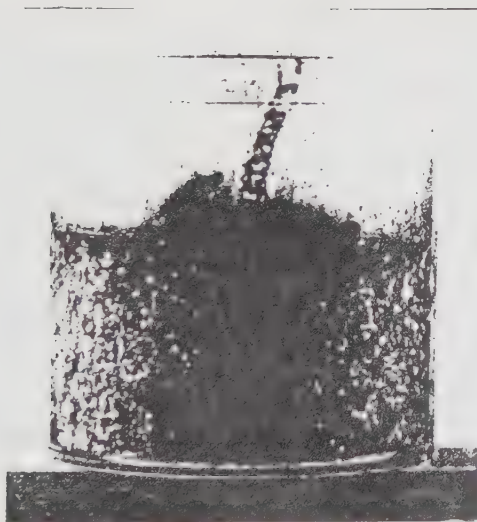


Fig. 3 - Cylindrical 572 cm³ (9 cm $\varnothing$ x 9 cm height) box used as a container for Termitidae species. This photo was taken of *Microcerotermes championi* after 3 weeks test period. The box contains 25 g vermiculite with a water content of 300 per cent.

substrate and water was thoroughly mixed in the humus soil and vermiculite. For *N. nigriceps* 3 g nest material was also spread on the surface of the substrate (humus soil).

2.3.4. Fodder blocks

Pine sapwood (*Pinus sylvestris* L.) was used as food for the *Rhinotermitidae*, *Kalotermitidae* and *Termopsidae* species while the *Termitidae* species were tested with birch wood (*Betula verrucosa* Ehrh.). The wood specimens used were all of the same growth quality. They were cut transversely to the wood fibre of sapwood planks which were cut tangentially from the stem. For the *K. flavicollis* tests, wood pieces of 15 mm x 15 mm x 25 mm were used while for all the other species wood blocks of 25 mm x 25 mm x 15 mm were supplied. The wood blocks were dried for five hours at 105°C, cooled for one hour in an exsiccator and then weighed. Before the wood pieces were used for the tests they were wetted with 30 to 50 % water (water % calculated from dry weight of wood pieces). The wood blocks were put on the surface of the substrate.

2.3.5. Group composition

Each species had a characteristic number and weight of insects used in the tests but these data varied from species to species. The numbers of animals in each test group are indicated in table 2. For each test (vermiculite) three parallels were used except for those of *N. nigriceps* (humus soil) for which four parallels were used.

2.3.6. Room temperature and relative humidity

R. flavipes, *H. indicola* and *C. formosanus* were tested at 26°C and 90 % $\pm$ 1 % relative humidity, *K. flavicollis* at 26°C and 98 to 99 % relative humidity, *M. championi* at 28°C and 95 to 98 % relative humidity, *N. nigriceps* at 30°C and 98 to 99 %

Table 2

Group composition, weight of each group and culture temperature of tested species.

Species	Group composition			Weight of each group (Ø) mg	Culture temp.
	W ¹⁾	S ²⁾	N ³⁾		
K. flavicollis	50	-	-	275 - 280	26°C
Z. angusticollis	15	-	-	450 - 455	20°C
H. indicola	500	5	2	650 - 660	30°C
R. flavipes (from Hamburg)	300	2	3	760 - 770	26°C
C. formosanus	320	80	-	1000 - 1010	30°C
M. championi	815	10	-	1500 - 1510	28°C
N. nigriceps	635	190	-	3990 - 4010	30°C

1) W = Worker

2) S = Soldier

3) N = Nymph

relative humidity and *Z. angusticollis* at 20°C and 98 to 99 % relative humidity.

2.3.7. Inspections

Because of the various modes of living of different species of termites - one stayed at the surface, another went to the bottom, while the third changed its residence - the following special methods were necessary for watching the insects in the containers during the tests.

- *K. flavicollis*, *Z. angusticollis* were observed from the surface of the substrate.
- *N. nigriceps* was observed from the surface as well as from the bottom of the substrate.
- The rest of the tested species were mostly observed from the bottom of the substrate.

Evaporated water was added weekly and the amount was determined after weighing the containers. The decrease in the weight of the containers due to the feeding of the insects was neglected. The insects were controlled twice a week by noting and removing the dead groups.

With the exception of *N. nigriceps* the feeding activity was measured after 4, 8 and 16 weeks. At every test control the wood blocks were taken out of the containers by removing the vermiculite and the insects and they were weighed immediately to determine their water content. The dry weight of the wood specimens was determined as described above. After four and eight weeks control the wood blocks were returned to the test containers after giving 30 to 50 % water. The percentage of water contents in the wood blocks was calculated as follows:

$$\frac{W_w \text{ 1) } - W_d \text{ 2)}}{W_d} \times 100 = \% \text{ of } H_2O \text{ contents in the wood}$$

1) W_w = wet weight of wood

2) W_d = dry weight of wood

The tests with *N. nigriceps* were stopped after 4 respectively 12 weeks for determining the feeding quantity as well as the number and weight of the living insects.

As the *K. flavicollis* and *Z. angusticollis* were always present on or inside the wood blocks or on the surface of the substrate but not in the substrate, it was possible to collect all the data at every observation (0 to 4 and 5 to 8 weeks) such as feeding quantity, weight and number of living insects. After 8 weeks the dead insects were substituted by new insects. In the case of *K. flavicollis* the wood blocks were splitted at each observation because the insects excavated in the wood pieces. Therefore it was necessary to add new wood blocks with this species at every observation.

Decrease in the weight of wood at every control showed activities of termites. At the end of the test after 16 weeks the weight and number of living insects was determined to know the change in groups as compared with the beginning of the test.

Table 3

Details of the method used for the species of termites tested

Species	Test conditions					Test period (weeks)		
	Temp. R.H. ¹⁾ (%)	Substrate	Substrate weight	H ₂ O content (%)	feeding wood species size (mm)			
K. flavi-collis	26°C	98/99	Vermiculite	15 g	50,100,200, 300,350,400	Pine sap-wood (P. sylvestris) 25	15 x 15 x 25 x 25 x 15	1 to 4 5 to 8 9 to 16
Z. angusti-collis	20°C	"	"	"	100,200, 300,350,400	"	"	"
H. indicola	26°C	90	"	"	"	"	"	"
R. flavipes	"	"	"	"	"	"	"	"
C. formo-sanus	"	"	"	"	"	"	"	"
M. cham-pioni	28°C	95/98	"	25 g	"	Birch wood (B. verrucosa Ehrh.)	"	"
N. nigri-ceps	30°C	98/99	humus soil	150 g	26/30/34/ 38/42	"	"	1 to 4 1 to 12

1) R.H. = Relative humidity

3. EXPERIMENTS AND RESULTS

3.1. Effect of relative humidity upon the survival of the termites under starvation conditions

3.1.1. Results with different species and castes of termites

3.1.1.1. *Neotermes jouteli* (Banks)

Five middle-sized (72.5 mg) pseudergates were supplied for each group and four replications were taken at each stage of relative humidity of the air. *Neotermes jouteli* showed an increasing average time of survival between 33 and 98 % relative humidity (Fig. 4), from 15.9 days at 33 % relative humidity up to the highest average survival of 31.5 days at 98 % relative humidity. At a lower atmospheric moisture (33 to 75 % relative humidity) the average survival was increased more rapidly than at higher relative humidity stages (85 to 98 %). Increasing relative humidity up to 100 % proved to be fatal for the insects and they showed an average survival of 25.5 days.

The last pseudoworker died after 20 days at 33 % and after 29 days at 63 % relative humidity, but at 98 % relative humidity all the insects were dead after 64 days (Table 4). These tests showed that 90 to 99 % relative humidity was the optimum for *Neotermes jouteli*. At 93 %, 98 % and 100 % relative humidity *N. jouteli* showed cannibalism during the first 3 weeks of the investigations.

Fig. 4 - Average survival of pseudoworkers of *Neotermes jouteli*, *Kaloterme flavicollis*, *Cryptotermes dudleyi* at 26°C and *Zootermopsis angusticollis* at 20°C under starvation conditions in relation to relative humidity.

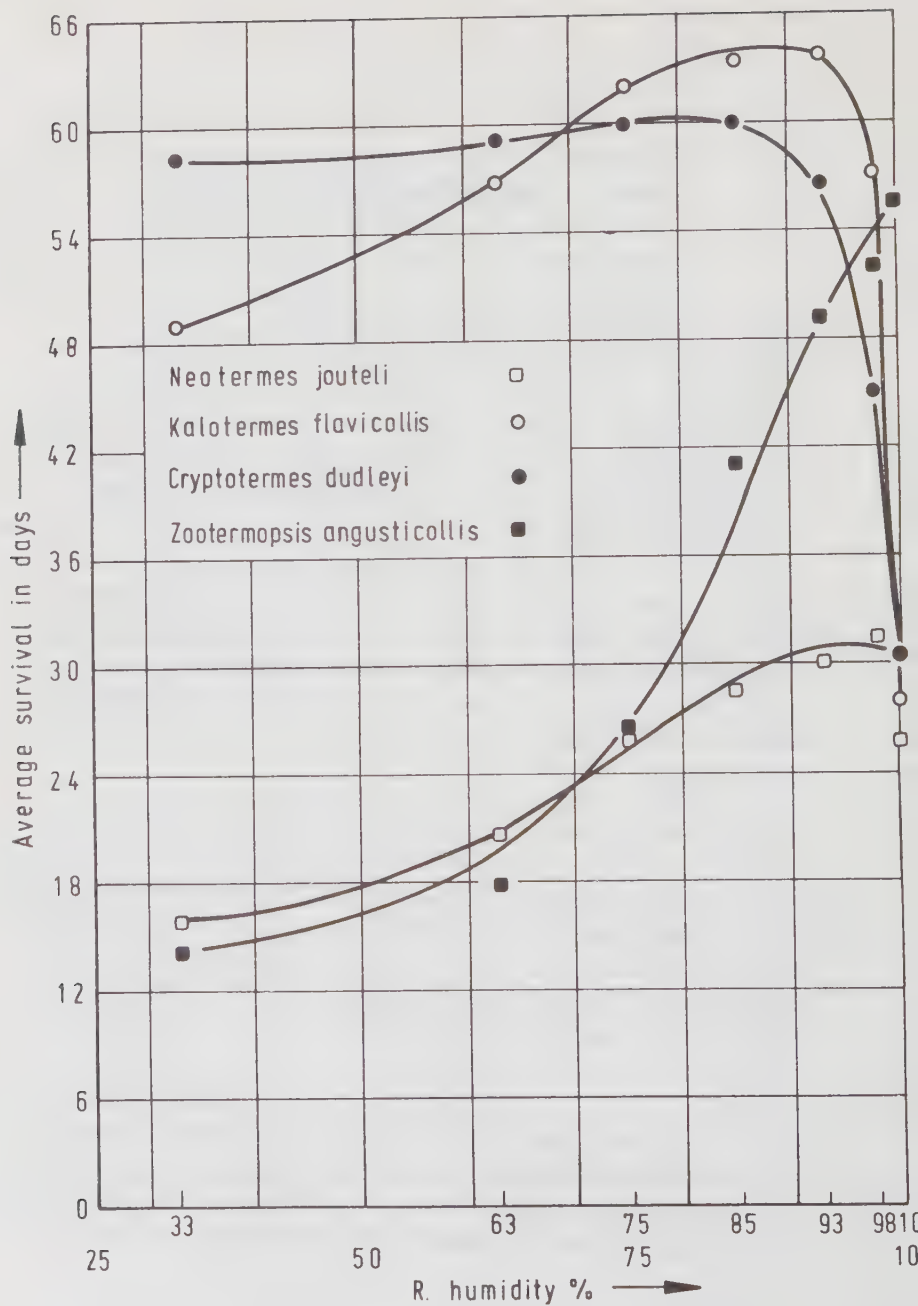


Fig. 4

Survival of pseudoworkers of *Neotermes jouteli*, *Kaloterms flavicollis*, *Cryptotermes dudleyi* (at 26°C) and *Zootermopsis angusticollis* (at 20°C) under starvation conditions in relation to the relative humidity

- 31 -

a) 5 individuals in each test group and 4 replications
C. dudleyi only 3 replications at 100 % relative humidity

3.1.1.2. *Kaloterme flavicollis* (Fabricius)

Five middle-sized (27.5 mg) pseudoworkers of *Kaloterme flavicollis* were taken in each group and 4 replications were supplied at each stage of atmospheric moisture.

Kaloterme flavicollis pseudoworkers showed an average survival of 49.2 days at 33 % relative humidity, which was raised with the increase of relative humidity up to 63.9 days at 93 % relative humidity. With the increase of the relative humidity from 93 to 98 % the insects showed a gradual reduction in the average survival and from 98 to 100 % relative humidity the average survival of insects was very markedly decreased (Table 4), e.g. at 98 and 100 % relative humidity the average survival of insects was 57.2 and 28.2 days respectively.

At 33 % and 100 % relative humidity all the pseudoworkers were dead within 66 and 45 days respectively. But the last pseudoworker died after 129 days at 85 % relative humidity.

The curve of the average longevity was raised gradually from 33 to 75 % relative humidity and very slowly from 75 to 93 % relative humidity. But between 93 and 100 % relative humidity the average longevity curve descended very rapidly (Fig. 4). The optimum range of relative humidity for this species was between 80 and 95 % relative humidity. *Kaloterme flavicollis* showed cannibalism at 93 and 98 % relative humidity.

At 75, 85, 93 and 98 % relative humidity imagines were developed in some of the groups after 6 to 8 weeks. These imagines were expelled out of the groups before they were eaten by the pseudoworkers.

3.1.1.3. *Cryptoterme dudleyi* Banks

Five middle-sized (30.5 mg) pseudoworkers were supplied in each group and four replications were used at each stage of

relative humidity, except at 100 % relative humidity where only three replications were taken.

Cryptotermes dudleyi showed more resistance at a lower relative humidity (33 to 85 %) than at a higher relative humidity (85 to 100 %). At 33 % relative humidity the insects showed an average survival of 58.8 days and with the increase of the relative humidity up to 85 % the insects showed a very slight increase in the rate of survival (59.9 days at 85 % relative humidity) (Table 4). But above 85 % relative humidity the average longevity of *Cryptotermes dudleyi* was reduced. At 100 % relative humidity *Cryptotermes dudleyi* showed the minimum average survival of 30.5 days. The last pseudoworker of this species died after 114 days at 63 % relative humidity. At 33 and 100 % relative humidity all the insects died within 100 and 35 days respectively.

The curve of the average survival was very slowly raised from 33 to 85 % relative humidity. But with an increase of the relative humidity from 85 to 100 % the average survival curve descended very quickly (Fig. 4). These experiments showed that 33 to 85 % relative humidity was suitable for the survival of the insects under starvation conditions. At 98 to 100 % relative humidity the insects showed cannibalism during the first four weeks of the experiment.

3.1.1.4. *Zootermopsis angusticollis* (Hagen)

Five middle-sized (188 mg) pseudoworkers were selected for each group and 4 replications were taken at each stage of relative humidity.

Zootermopsis angusticollis showed a minimum average survival of 14.7 days (33 % relative humidity) which increased with the raising of the relative humidity up to 26.7 days at 75 % relative humidity and 55.5 days at 100 % relative humidity (Table 4). The last pseudoworker was dead after 77 days at 100 % relative humidity, but at 33 % and 75 % relative humidity

dity all the insects were dead within 24 and 45 days respectively.

The increase in the survival of insects with the raising of the atmospheric moisture was low at 33 to 75 % relative humidity in comparison with 75 to 100 % relative humidity (Fig. 4). 100 % relative humidity was the optimum for the pseudoworkers of *Zootermopsis angusticollis*. Thus, this termite can be called stenohygrous. Pseudoworkers showed cannibalism during the investigations from 63 to 100 % relative humidity.

3.1.1.5. *Heterotermes indicola* (Wasmann)

Tests were done with workers and soldiers of *heterotermes indicola* from 26°C and 30°C cultures. 30 workers (36 mg) and 5 soldiers (6 mg) were selected for each group. Five replications of workers and three replications of soldiers were taken at each stage of relative humidity.

Workers from 30°C culture

The workers showed an increasing average survival of 3.9 days (33 % relative humidity) up to 33.4 days (100 % relative humidity) (Table 5). The highest survival of workers was 40 days at 98 % relative humidity. At 33 % and 85 % relative humidity all the workers were dead within 9 and 16 days respectively.

The average longevity of insects increased slowly between 33 and 85 % relative humidity, whereas, from 85 to 100 % relative humidity the average longevity was increased very quickly (Fig. 5).

Workers from 26°C culture

The workers from 26°C cultures showed a minimum average survival of 3.5 days at 33 % relative humidity. At 100 % relative humidity the average survival was increased up to a maximum

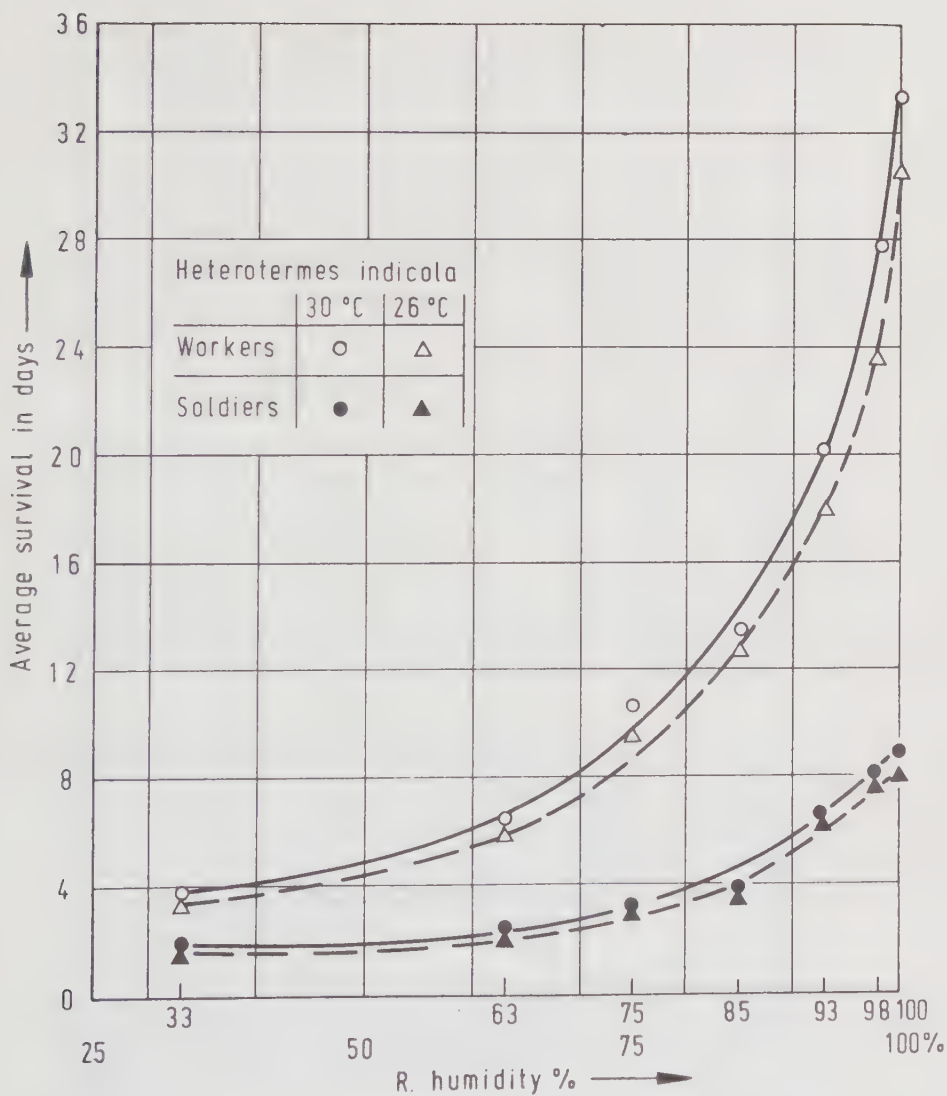


Fig. 5 - Average survival of grouped workers and grouped soldiers of *Heterotermes indicola* (from 30 and 26°C cultures) under starvation conditions in relation to relative humidity at 26°C.

Table 5

Survival of workers and soldiers of *Heterotermes indicola* (from 26 and 30°C cultures) at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	Workers a)				Soldiers b)			
	30°C culture	26°C culture	30°C culture	26°C culture	30°C culture	26°C culture	30°C culture	26°C culture
	Range	Average	Range	Average	Range	Average	Range	Average
33	2-9	3.9	2-6	3.5	1-2	1.9	1-2	1.7
63	2-9	6.5	1-8	5.9	1-3	2.4	2-3	2.3
75	6-12	10.7	7-11	9.5	2-5	3.4	2-5	3.0
85	10-16	13.5	7-16	12.7	3-5	3.9	2-5	3.6
93	10-23	20.3	12-21	17.9	2-8	6.6	4-8	6.3
98	14-40	27.8	14-28	23.6	3-10	8.2	5-11	7.6
100	14-37	33.4	23-35	30.5	4-11	8.9	4-11	8.0

a) 30 individuals in each test group and 5 replications

b) 5 individuals in each test group and 3 replications

of 30.5 days. The last workers from the 26°C culture was dead after 35 days at 100 % relative humidity. Raising of the curve with the increase of relative humidity was the same as described for workers from the 30°C culture.

Workers from 30°C culture were somewhat more resistant against desiccation than workers from 26°C culture. The difference in the average longevity of workers (from 26°C and 30°C culture) increased with the raising of the atmospheric moisture (Fig. 5).

Soldiers from 30°C culture

Soldiers showed an increasing average survival from 1.9 days at 33 % relative humidity up to 8.9 days at 100 % relative humidity. At 85 % relative humidity the average survival of soldiers was 3.9 days (Table 5). The last soldier died after 11 days at 100 % relative humidity. At 85 to 100 % relative humidity the average survival of soldiers was raised (Fig. 5) somewhat more quickly than at 33 to 85 % relative humidity.

Soldiers from 26°C culture

The lowest average survival of soldiers was 1.7 days at 33 % relative humidity which was increased up to 3.6 days at 85 % relative humidity. But the maximum average survival was 8.5 days at 100 % relative humidity (Table 5). The increase in the average longevity curve was the same as described above for 30°C soldiers.

Soldiers from both the cultures showed about the same desiccation resistance. Comparison between workers and soldiers from both the cultures showed that workers were more resistant against drying than soldiers. The difference between the average survival curve (Fig. 5) of soldiers and workers was increased with raising the percentage of the atmospheric moisture.

These tests showed that 100 % relative humidity is the optimum for *Heterotermes indicola*. This termite can be called steno-

hygrous. At 93 to 100 % relative humidity workers (26°C and 30°C cultures) showed cannibalism.

3.1.1.6. *Coptotermes formosanus* (Shiraki)

In the case of *C. formosanus* the investigations were carried out with workers (grouped and isolated), soldiers (grouped and isolated) and heterogenous groups (workers and soldiers grouped together).

Grouped workers

Twenty workers were used in each group and five replications were supplied at each stage of the relative humidity. The average weight of each group was about 54 mg. The grouped workers showed a minimum average survival of 2.1 days at 33 % relative humidity and a maximum average survival of 15.4 days at 100 % relative humidity (Table 6). The highest survival of workers was 20 days at 100 % relative humidity. At 33 % and 85 % relative humidity all the workers were dead within 3 and 6 days respectively.

The average longevity of the insects increased slowly between 33 and 85 % relative humidity (Fig. 6), but from 85 to 100 % relative humidity the average longevity increased very rapidly.

Isolated workers

Ten isolated workers were taken at each stage of the relative humidity. It has been found that the isolated workers showed an increasing average survival from 1.4 days at 33 % relative humidity up to 10.5 days at 100 % relative humidity (Table 6). At 33 % relative humidity all the insects were dead within two days. But at 100 % relative humidity the last worker died after 15 days. The raising of the curve (Fig. 6) with an increase of the relative humidity was the same as described above for the grouped workers.

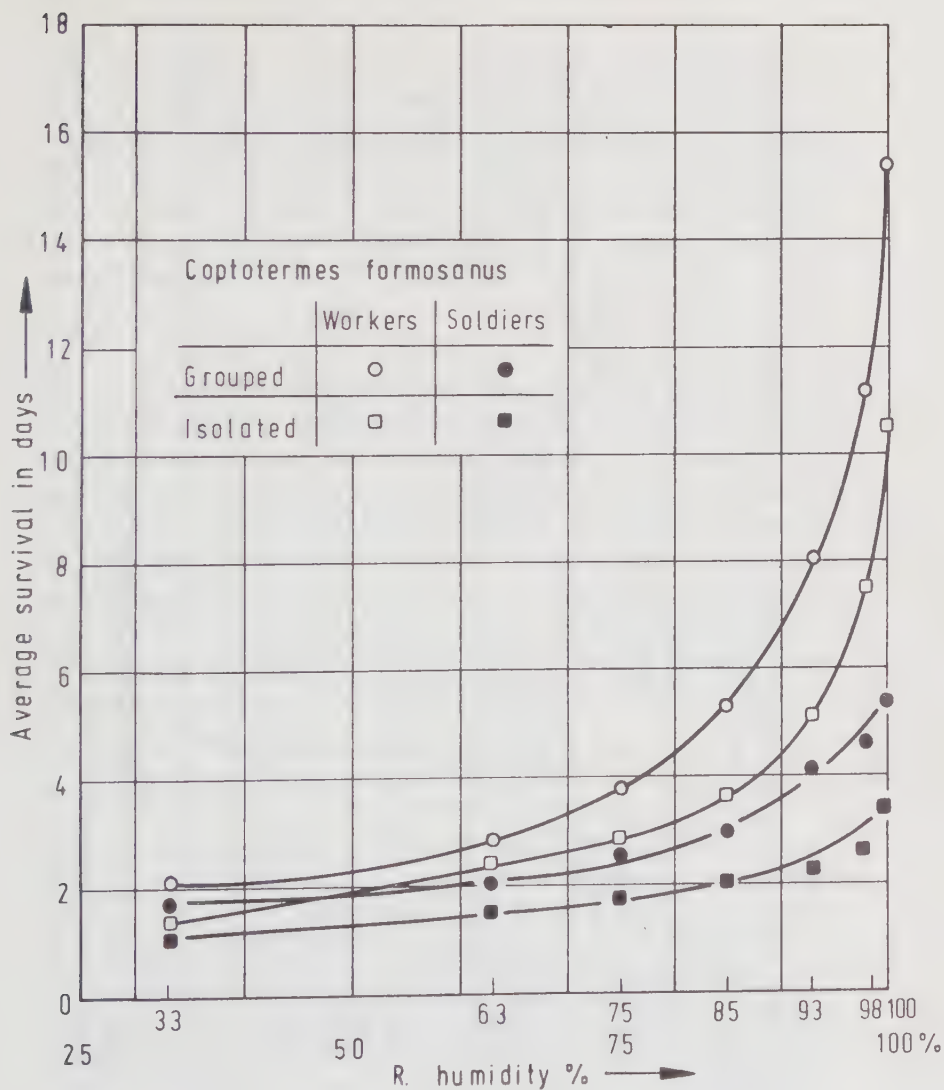


Fig. 6 - Average survival of workers (grouped and isolated) and soldiers (grouped and isolated) of *Coptotermes formosanus* under starvation conditions in relation to relative humidity at 26°C.

Table 6

Survival of grouped and isolated workers and soldiers of *Coptotermes formosanus* (at 26°C) under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	Workers				Soldiers			
	Grouped a)		Isolated b)		Grouped a)		Isolated b)	
	Range	Average	Range	Average	Range	Average	Range	Average
33	1-3	2.1	1-2	1.4	1-3	1.7	0-1	1.0
63	2-4	2.9	2-3	2.5	1-3	2.0	1-2	1.5
75	2-6	3.8	2-3	2.7	2-6	2.6	1-2	1.8
85	3-6	5.3	3-4	3.7	2-6	2.9	1-3	2.1
93	6-10	8.1	2-6	5.1	2-8	4.2	2-3	2.3
98	10-15	11.2	5-11	7.5	3-8	4.6	2-3	2.6
100	10-20	15.4	3-15	10.5	2-10	5.4	2-5	3.4

a) 20 individuals in each test group and 5 replications

b) 10 individuals kept isolated

These investigations have shown that grouped workers are more resistant against drying than isolated workers. The difference between the average survival of grouped and isolated workers increased slowly from 33 to 75 % relative humidity, whereas, from 75 to 100 % relative humidity the grouped workers showed a rapid increase in the average survival compared to the isolated workers.

Grouped soldiers

Twenty individuals (66 mg) were kept in each group and five replications were used at each stage of relative humidity. The minimum and maximum average survival of 20 soldiers was 1.7 and 5.4 days at 33 and 100 % relative humidity respectively. At 85 % relative humidity the soldiers showed an average survival of 2.9 days. At 33 and 85 % relative humidity all the soldiers were dead within 3 and 6 days respectively (Table 6). But the last soldier survived up to 10 days at 100 % relative humidity. As shown in Fig. 6 the average survival of insects increased gradually with raising the atmospheric moisture.

Isolated soldiers

Ten isolated soldiers were used at each stage of the relative humidity. Isolated soldiers showed a very slow increase of the average survival from 1.0 day at 33 % relative humidity up to 3.4 days at 100 % relative humidity (Table 6). The highest survival of isolated soldiers was five days at 100 % relative humidity. The average longevity curve was increased slowly (Fig. 6) with raised relative humidity (from 33 to 100 %). It has been found that grouped soldiers were more resistant against desiccation than isolated soldiers. But the difference between the average longevity of grouped and isolated soldiers was more marked at 85 to 100 % relative humidity than at lower stages of relative humidities.

Workers (isolated or grouped) showed more resistance to desiccation than soldiers (grouped and isolated). The difference between the average longevity of workers and soldiers was increased more distinctly from 85 to 100 % relative humidity.

From 33 to 75 % relative humidity the difference in the average survival of isolated and grouped workers was about equal to the difference in the average survival of isolated and grouped soldiers, whereas, at 75 to 100 % relative humidity the difference between the average survival of isolated and grouped workers increased rapidly in comparison with the difference between the average longevity of isolated and grouped soldiers (Fig. 6).

Heterogenous groups (workers and soldiers grouped together)

For these tests 20 workers and 10 soldiers were put together in each group and five replications were provided at each stage of relative humidity.

Workers

The average survival of workers was 2.1 days at 33 % relative humidity and 5.1 days at 85 % relative humidity. But the insects showed the maximum average survival of 11.0 days at 100 % relative humidity (Table 7). At 33 % relative humidity all the workers were dead within 3 days and the longest survival of workers was 13 days at 100 % relative humidity. The curve of the average longevity was raised slowly from 33 to 75 % relative humidity compared to 75 to 100 % relative humidity (Fig. 7).

Soldiers

The soldiers showed an average survival of 1.8 days at 33 %, 4.1 days at 85 % and 6.4 days at 100 % relative humidity (Table 7). At 33 and 85 % relative humidity all the soldiers were dead within 2 and 6 days respectively. The last soldier

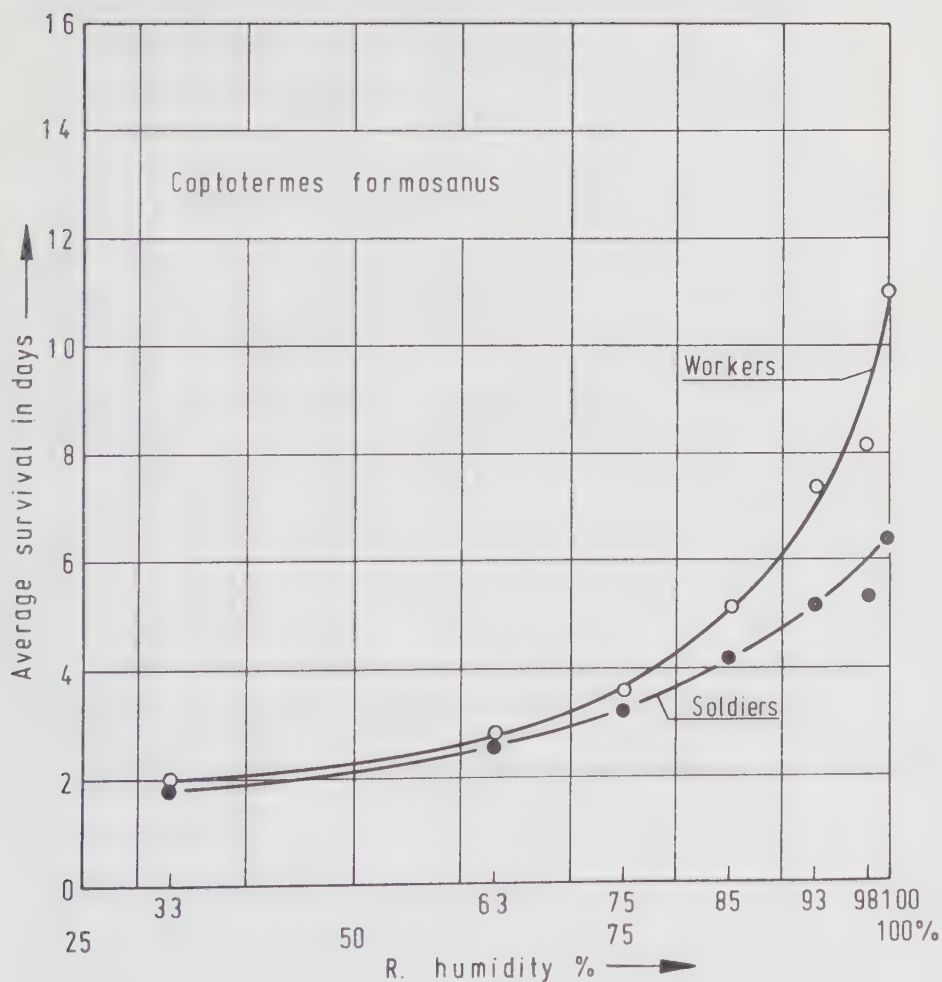


Fig. 7 - Average survival of workers and soldiers of *Coptotermes formosanus* under starvation conditions in relation to relative humidity at 26°C when kept in heterogenous groups (20 workers and 10 soldiers together in each group).

Table 7

Survival of workers and soldiers of *Coptotermes formosanus* kept in heterogenous groups (20 workers and 10 soldiers together in each group) at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days			
	Workers		Soldiers	
	Range	Average	Range	Average
33	2-3	2.1	1-2	1.8
63	2-4	2.9	2-4	2.6
75	2-6	3.6	3-4	3.2
85	3-6	5.1	3-6	4.1
93	4-10	7.4	3-8	5.2
98	2-11	8.2	2-10	5.2
100	6-13	11.0	2-11	6.4

5 replications at each stage of relative humidity

was dead after 11 days at 100 % relative humidity. The curve of the average longevity was increased gradually with the increase of relative humidity (Fig. 7).

At 33 to 75 % relative humidity desiccation resistance of soldiers and workers (in heterogenous groups) was about similar, whereas, from 75 to 100 % relative humidity the average survival of workers was more rapidly increased than the average survival of soldiers (Fig. 7).

Desiccation resistance of soldiers in heterogenous groups (Table 7) was somewhat higher than the desiccation resistance of homogenous groups of soldiers (Table 6). At 93 to 100 % relative humidity the average survival of workers in heterogenous groups (Table 7) was less than the average survival of homogenous groups of workers (Table 6). 100 % relative humidity was the optimum for *C. formosanus* and no cannibalism was observed during the investigations.

3.1.1.7. *Coptotermes niger* Snyder

To study the desiccation resistance of *C. niger* the investigations were carried out with grouped workers, grouped soldiers and heterogenous groups (workers and soldiers grouped together).

Grouped workers

Twenty individuals were kept in each group and 5 replications were supplied at each stage of relative humidity. The average weight of each group was about 72 mg. The minimum average survival of 20 workers was 1.2 days at 33 % relative humidity and the maximum of the average survival was 7.7 days at 100 % relative humidity (Table 8). At 33 % relative humidity all workers were dead within 2 days and at 85 % relative humidity within 5 days. The highest longevity of workers was 10 days at 100 % relative humidity. From 33 to 85 % relative humidity the insects showed a very slow increase in the average longe-

vity but the average longevity was raised fast from 85 to 100 % relative humidity (Fig. 8). The grouped workers showed cannibalism at 93 to 100 % relative humidity.

Grouped soldiers

Twenty soldiers (52 mg) in each group and five replications were used at every stage of the relative humidity.

Soldiers showed an increasing average survival from 1.5 days (33 % relative humidity) up to 5.2 days at 100 % relative humidity (Table 8). At 33 % relative humidity 100 % mortality was observed within 2 days. The longest survival time of soldiers was 9 days at 98 % relative humidity. As shown in Fig. 8 the average longevity of soldiers was raised slowly at 33 to 85 % relative humidity, whereas, at 85 to 100 % relative humidity the average longevity increased rapidly.

The comparison between desiccation resistance of grouped workers and grouped soldiers showed that from 33 to 75 % relative humidity soldiers were somewhat more resistant than workers and at 75 to 85 % relative humidity both castes showed about the same resistance. But from 85 to 100 % relative humidity the average longevity of workers increased faster than the average longevity of soldiers.

Heterogenous groups

Twenty workers and 10 soldiers were kept together in each group and 5 replications were used at each stage of the relative humidity.

Workers

The workers showed an average survival of 1.0 days at 33 % relative humidity which was raised with the increase of relative humidity up to 2.2 days at 85 % and 5.9 days at 100 % relative humidity. The highest survival period of workers was 8 days at 100 % relative humidity. But at 33 and 85 % relative

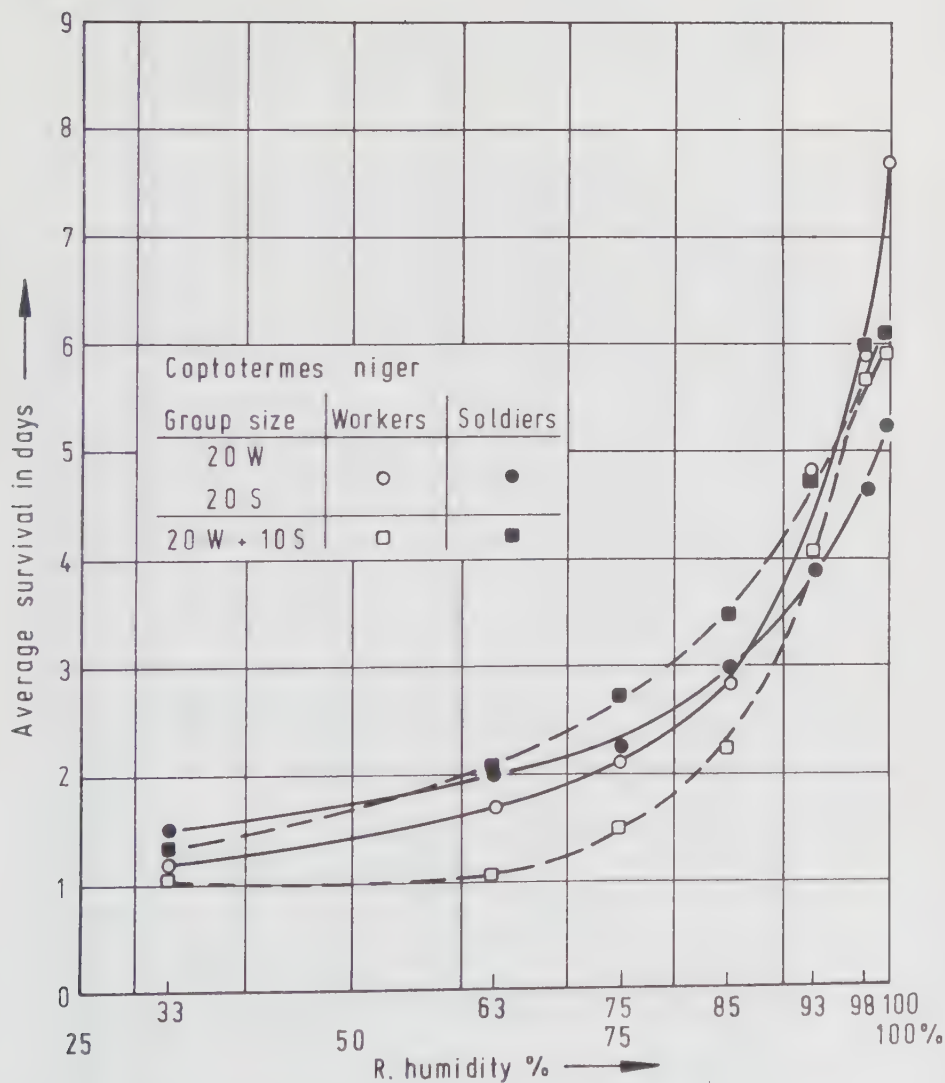


Fig. 8 - Average survival of grouped workers, grouped soldiers and heterogenous groups (20 workers and 10 soldiers kept together in each group) of *Coptotermes niger* under starvation conditions in relation to relative humidity at 26°C.

Table 8

Survival of grouped workers, grouped soldiers and heterogeneous groups (20 workers and 10 soldiers together in each group) of *Coptotermes niger* at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	Homogenous groups a)				Heterogenous groups b)			
	Workers		Soldiers		Workers		Soldiers	
	Range	Average	Range	Average	Range	Average	Range	Average
33	1-2	1.2	1-2	1.5	1-2	1.0	1-2	1.4
63	1-2	1.7	1-3	2.0	1-2	1.2	1-3	2.1
75	2-3	2.1	2-3	2.2	1-2	1.5	1-4	2.7
85	2-5	2.8	2-5	2.9	2-4	2.2	3-4	3.5
93	3-7	4.8	3-8	3.9	2-6	4.1	2-6	4.8
98	2-9	5.9	2-9	4.6	3-6	5.7	4-6	5.9
100	3-10	7.7	3-8	5.2	3-8	5.9	4-8	6.1

a) 20 individuals in each test group and 5 replications
 b) 20 workers + 10 soldiers in each test group and 5 replications

humidity all the workers were dead within 2 and 4 days respectively (Table 8). The curve of the average longevity (Fig. 8) was raised gradually with the increase of the relative humidity.

Soldiers

The soldiers showed a minimum average longevity of 1.4 days at 33 % relative humidity. At 85 % relative humidity the soldiers showed an average survival of 3.5 days. The maximum of the average survival of soldiers was 6.1 days at 100 % relative humidity (Table 8). At 33 and 85 % relative humidity all the soldiers were dead within 2 and 4 days respectively. But the last soldier survived up to 8 days at 100 % relative humidity. The curve of the average survival (Fig. 8) was continuously raised with the increase of the relative humidity from 33 to 98 % relative humidity. But at 98 to 100 % relative humidity the curve of the average longevity was raised very slowly.

In heterogenous groups soldiers survived slightly longer than workers at all stages of the relative humidity. At 63 to 100 % relative humidity the soldiers in heterogenous groups survived somewhat longer than homogenous groups of soldiers. But the average survival of workers in heterogenous groups was less than the average survival of homogenous groups of workers.

100 % relative humidity proved to be the optimum for the workers and soldiers of *C. niger*.

3.1.1.8. *Reticulitermes flavipes* (Kollar)

3.1.1.8.1. *Reticulitermes flavipes* from Charleston

To investigate the susceptibility of this termite, the insects were taken for the tests in the following group compositions: grouped workers, grouped soldiers and heterogenous groups (workers and soldiers grouped together).

Grouped workers

Twenty workers were kept in each group, with three replications at each stage of atmospheric moisture.

The workers showed the lowest average longevity of 1.2 days at 33 % relative humidity (Table 9), which was raised slowly up to 3.8 days at 93 % relative humidity. But the maximum average survival of workers increased up to 9.1 days at 100 % relative humidity. At 33 and 93 % relative humidity all the workers were dead within 2 and 6 days respectively. But at 100 % relative humidity the last worker died after 13 days.

As shown in Fig. 9 the average survival of workers was raised slowly from 33 to 93 % relative humidity, but at 93 to 100 % relative humidity the average survival of workers increased rapidly.

Very little cannibalism was observed at 93 to 100 % relative humidity.

Grouped soldiers

Five soldiers were kept in each group and three replications were taken at each stage of relative humidity. The average weight of each group was about 18 mg.

The minimum and maximum average survival of soldiers was 1.3 days at 33 % and 7.2 days at 100 % relative humidity respectively. 100 % mortality was observed after 2 days at 33 % and after 8 days at 100 % relative humidity (Table 9). The curve of the average longevity (Fig. 9) was raised slowly from 33 to 98 % relative humidity. But between 98 and 100 % relative humidity the curve of the average longevity was raised more rapidly.

A comparison between the grouped workers and grouped soldiers showed that between 33 and 93 % relative humidity the soldiers were somewhat more resistant than workers, but from 93 to 100 % relative humidity workers revealed more resistance to desiccation than soldiers.

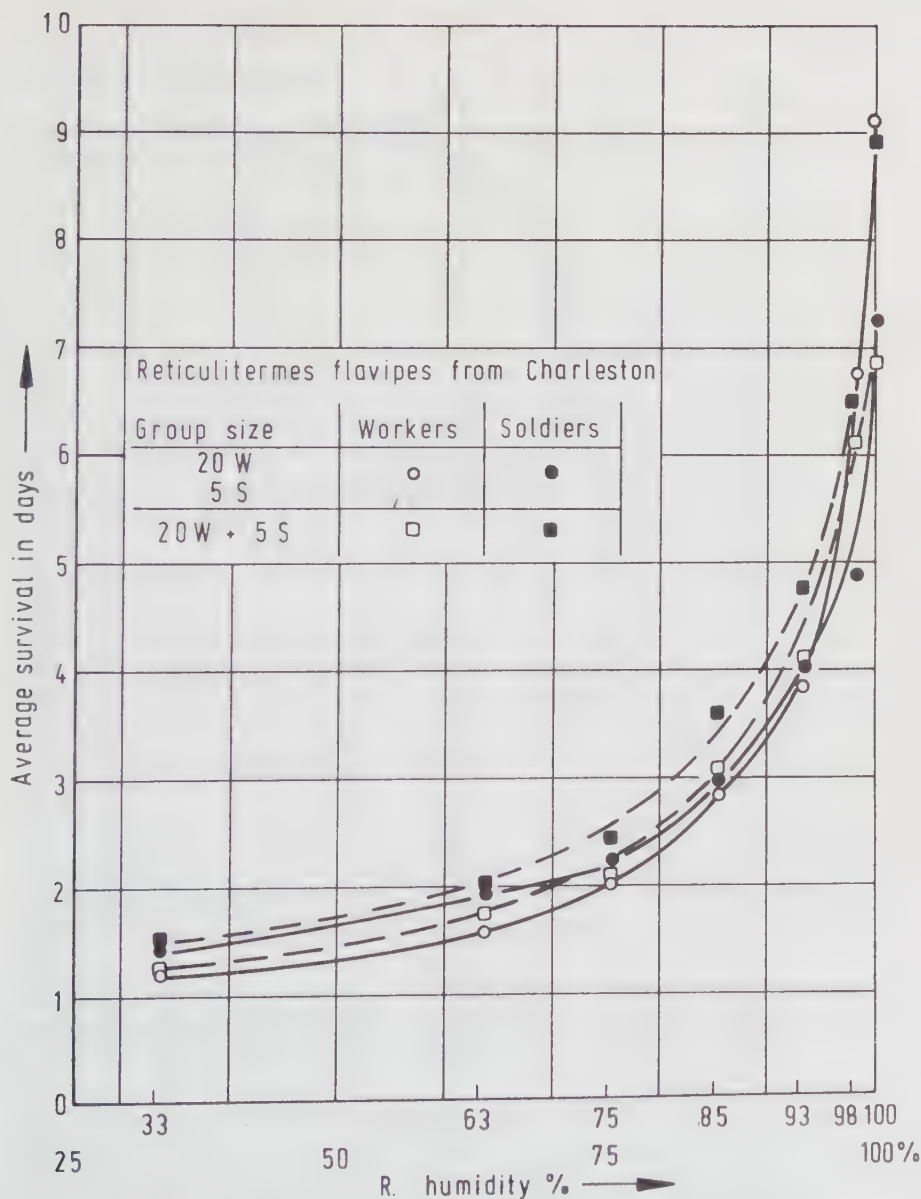


Fig. 9 - Average survival of grouped workers, grouped soldiers and heterogenous groups (20 workers and 5 soldiers in each group) of *Reticulitermes flavipes* from Charleston under starvation conditions in relation to relative humidity at 26°C.

Survival of grouped workers, grouped soldiers and heterogeneous groups (20 workers and 5 soldiers together in each group) of *Reticulitermes flavipes* from Charleston at 26°C under starvation conditions in relation to relative humidity.

- 20 individuals in each test group and 3 replications
- 5 individuals in each test group and 3 replications
- 20 workers + 5 soldiers in each test group and 3 replications

Heterogenous groups

Twenty workers and 5 soldiers were kept together in each group and 3 replications were used at each stage of relative humidity.

Workers

The workers showed an increasing average survival from 1.1 days (33 % relative humidity) up to 6.8 days (100 % relative humidity) (Table 9). At 33 and 100 % relative humidity all the workers were dead within 2 and 13 days respectively. The average survival was raised somewhat more rapidly at 93 to 100 % relative humidity than at 33 to 93 % relative humidity (Fig. 9).

Soldiers

The shortest average survival period of soldiers was 1.5 days at 33 % relative humidity. But the maximum average survival of soldiers was 8.9 days at 100 % relative humidity. At 33, 93 and 100 % relative humidity all soldiers were dead within 2, 6 and 13 days respectively.

In heterogenous groups the soldiers were somewhat more resistant against desiccation than workers at all stages of relative humidity except at 100 % relative humidity where the resistance of soldiers in relation to workers was more distinct.

Soldiers in heterogenous groups survived longer than the homogenous groups of soldiers. The difference was more obvious at higher stages of relative humidity.

At 98 to 100 % relative humidity the average survival of homogenous groups of workers was about 2 days longer than the average survival of workers in heterogenous groups. But between 33 and 98 % relative humidity no difference in the survival period was observed.

3.1.1.8.2. *Reticulitermes flavipes* from Hallein

To investigate the desiccation resistance of this termite, the experiments were carried out with nymphs and workers.

Workers

Ten workers (20 mg) were selected in each group and 3 replications were taken at each stage of atmospheric moisture. The workers showed the lowest and the highest average survival of 1.7 and 11.5 days at 33 and 100 % relative humidity respectively (Table 10). At 85 % relative humidity the average survival of workers was 4.4 days. At 33 % relative humidity all the insects were dead within 2 days and at 85 % relative humidity they were dead within 7 days. However, at 100 % relative humidity the last worker survived up to 15 days.

At 33 to 85 % relative humidity (Fig. 7) the insects showed a gradual increase in the average survival with the increase of the relative humidity but from 85 to 100 % relative humidity the average longevity of workers was raised rapidly. No cannibalism was observed during the investigations.

Nymphs

Five nymphs (21.5 mg) were kept in each group and 3 replications were supplied at each stage of relative humidity.

The minimum average survival of nymphs was 2.0 days at 33 % relative humidity which was increased up to 4.82 days at 85 % relative humidity. But the maximum average survival of nymphs was increased up to 12.6 days at 100 % relative humidity. The highest duration of survival of a nymph was 15 days at 100 % relative humidity. The raising of the survival curve with the increase of the relative humidity was about the same as described for the workers. No cannibalism of the nymphs was observed during the investigations.

A comparison between workers and nymphs showed that at lower (33 to 93 %) atmospheric moisture both castes revealed about

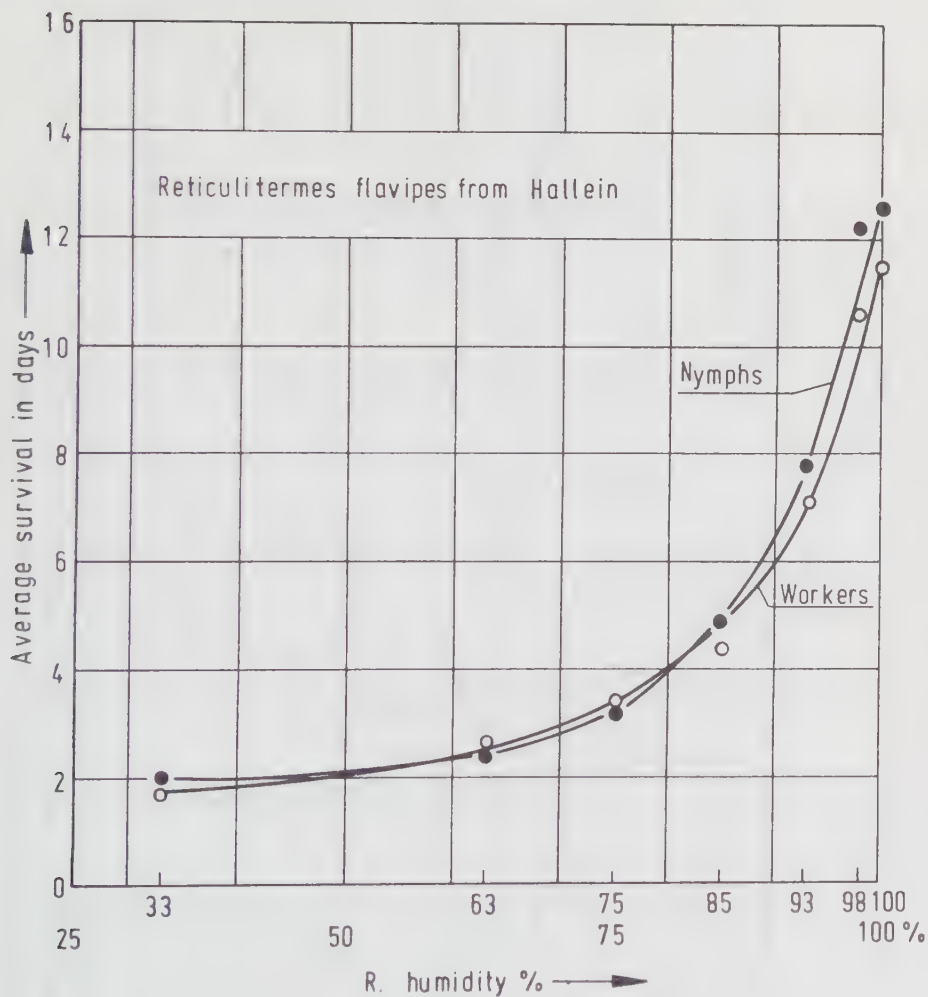


Fig. 10 - Average survival of grouped workers and grouped nymphs of *Reticulitermes flavipes* from Hallein under starvation conditions in relation to relative humidity at 26°C.

Table 10

Survival of grouped workers and grouped nymphs of *Reticulitermes flavipes* from Hallein and of grouped and isolated workers of *Reticulitermes flavipes* from Hamburg at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	R. flavipes from Hallein				R. flavipes from Hamburg			
	Grouped workers ^{a)}		Grouped nymphs ^{b)}		Grouped workers ^{a)}		Isolated workers ^{c)}	
	Range	Average	Range	Average	Range	Average	Range	Average
33	1-2	1.7	1-3	2.0	1-3	2.2	1-3	2.0
63	1-3	2.6	2-3	2.7	2-4	3.2	2-3	2.6
75	2-4	3.4	3-4	3.2	2-5	4.4	3-4	3.6
85	2-7	4.4	3-5	4.8	4-7	5.2	3-7	4.8
93	3-9	7.1	5-9	7.8	5-9	7.3	7-9	6.5
98	7-13	10.7	11-13	12.2	5-13	9.3	5-11	8.2
100	2-15	11.5	9-15	12.6	5-12	9.9	7-13	8.6

a) 10 individuals in each test group and 3 replications

b) 5 individuals in each test group and 3 replications

c) 5 individuals kept isolated

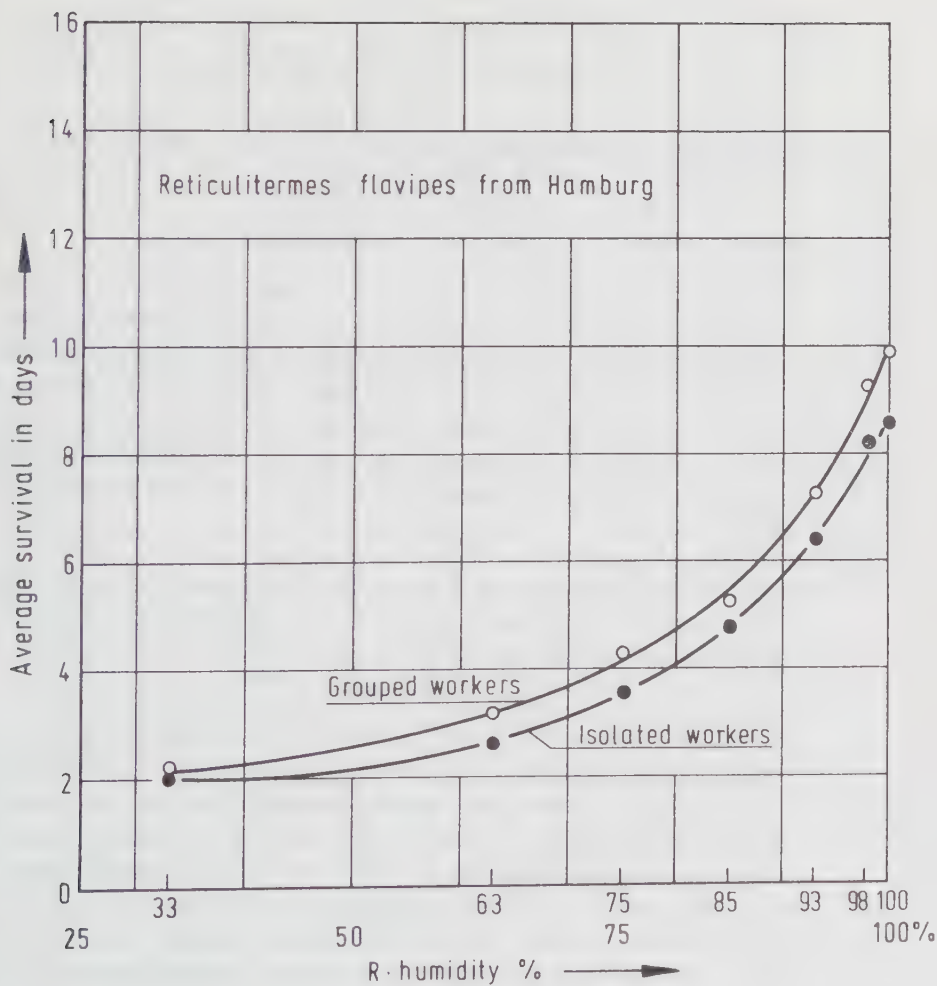


Fig. 11 - Average survival of grouped and isolated workers of *Reticulitermes flavipes* from Hamburg under starvation conditions in relation to relative humidity at 26°C.

the same resistance against desiccation but from 93 to 100 % relative humidity nymphs survived somewhat longer than workers.

3.1.1.8.3. *Reticulitermes flavipes* from Hamburg

Grouped and isolated workers of this termite were used for the tests.

Grouped workers

Ten workers (28 mg) were selected in each group and 3 replications were provided at each stage of relative humidity. The workers showed an increasing average survival from 2.0 days at 33 % relative humidity up to 9.9 days at 100 % relative humidity. At 33 and 85 % relative humidity all the insects died within 3 and 7 days respectively. But at 98 % relative humidity the upper limit of survival of workers was 13 days (Table 10).

The average longevity of insects was increased gradually between 33 and 85 % relative humidity and rapidly from 85 to 100 % relative humidity (Fig. 11).

Isolated workers:

Five isolated workers were taken at each stage of atmospheric moisture. The minimum and maximum average survival of isolated workers was 2.0 and 8.6 days at 33 and 100 % relative humidity respectively. The highest survival period of isolated workers was 2 days at 33 % relative humidity and 13 days at 100 % relative humidity (Table 10). The average survival curve was raised in the same way as in the case of grouped workers (Fig. 11).

At 33 % relative humidity the grouped and isolated workers showed about the same resistance against the desiccation. But from 63 to 100 % relative humidity the grouped workers revealed somewhat more resistance against drying than isolated ones.

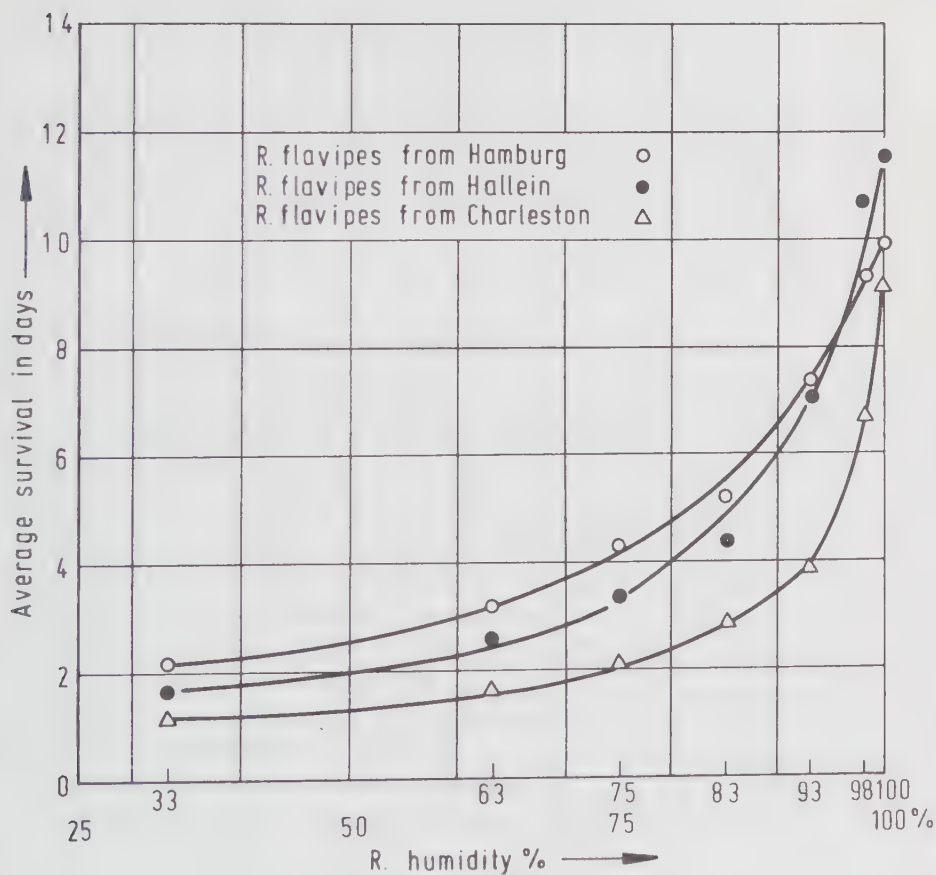


Fig. 12 - Comparison between the average survival of grouped workers of *Reticulitermes flavipes* from Charleston (USA), Hamburg and Hallein under Starvation conditions in relation to relative humidity at 26°C.

The comparison between *R. flavipes* from Charleston, Hallein and Hamburg showed that at lower atmospheric moisture (33 to 93 % relative humidity), *R. flavipes* from Hamburg survived longer than *R. flavipes* from Hallein and Charleston. But at higher atmospheric moisture the insects from Hallein showed slightly more average survival than *R. flavipes* from Hamburg and Charleston. At 100 % relative humidity *R. flavipes* from Hamburg and Charleston showed about the same average longevity. These studies proved that *R. flavipes* from Hamburg and Charleston were more similar to each other than *R. flavipes* from Hallein (Fig. 12).

3.1.1.9. *Reticulitermes hesperus* (Banks)

Ten workers (15 mg) were selected for each group and 3 replications were provided at each stage of atmospheric moisture. These insects showed lowest average longevity of 2.4 days at 33 % relative humidity which was increased slowly up to 6.7 days at 85 % relative humidity. Above 85 % relative humidity the average longevity of insects increased very quickly and at 100 % relative humidity average survival of 10 workers was 21.1 days. At 33 and 85 % relative humidity all the workers were dead within 4 and 9 days respectively. But the upper limit of survival period of workers was 28 days at 100 % relative humidity (Table 11). The curve of the average survival period (Fig. 13) raised slowly between 33 and 85 % and very rapidly between 85 and 100 % relative humidity. Cannibalism was observed at 98 to 100 % relative humidity. 100 % relative humidity proved to be the optimum for *R. hesperus*.

3.1.1.10. *Reticulitermes lucifugus* (Rossi)

3.1.1.10.1. *Reticulitermes lucifugus* from Favone

Ten workers (32 mg) were kept in each group, with 3 replications at each stage of relative humidity. The workers revealed the shortest average longevity of 1.7 days at 33 % relative hu-

Fig. 13 - Average survival of grouped workers of *Reticulitermes hesperus* and *Reticulitermes tibialis* under starvation condition in relation to relative humidity at 26°C.

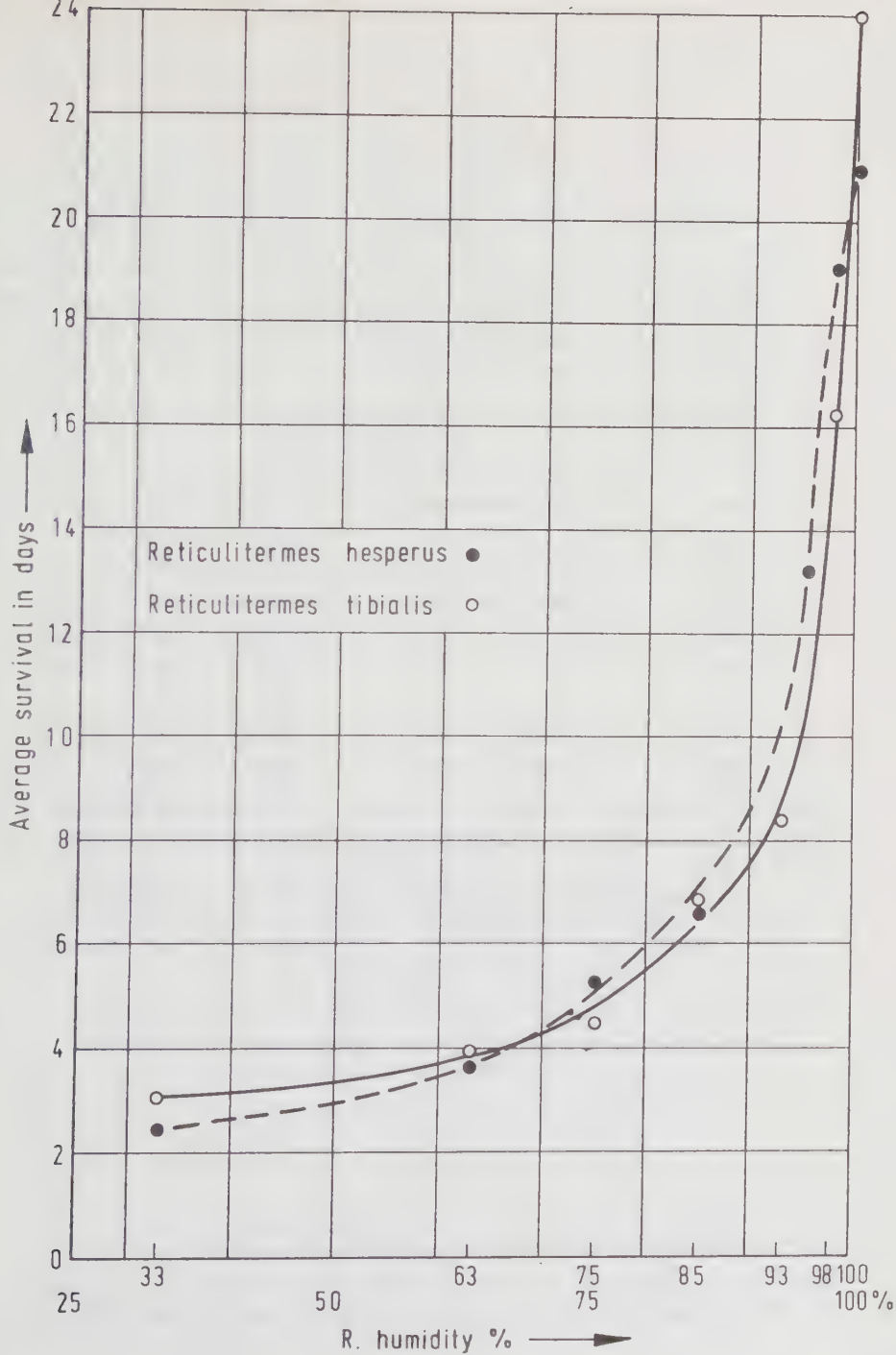


Fig. 13

Table 11

Survival of grouped workers of *Reticulitermes hesperus* and *Reticulitermes tibialis* at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days			
	R. hesperus		R. tibialis	
	Range	Average	Range	Average
33	1-4	2.4	2-4	3.1
63	2-5	3.8	2-4	3.9
75	3-6	5.3	4-6	4.5
85	4-9	6.7	6-9	6.9
93	7-16	13.2	4-13	8.4
98	9-26	19.1	2-22	16.2
100	9-28	21.1	4-35	24.0

10 individuals in each test group and 3 replications

midity. But at 100 % relative humidity the insects showed the maximum average survival of 18.4 days. At 33 and 85 % relative humidity 100 % mortality was observed after 3 and 7 days respectively. At 100 % relative humidity all the insects were dead within 26 days (Table 12). Average longevity of insects was increased very slowly from 33 to 85 % relative humidity (Fig. 14), whereas, between 85 and 100 % relative humidity average survival increased very distinctly. 100 % relative humidity proved to be the optimum for this species.

3.1.1.10.2. *Reticulitermes lucifugus* from Francavilla

To study the desiccation resistance of *R. lucifugus* from Francavilla, the tests were done with isolated and grouped workers under starvation conditions in relation to relative humidity.

Grouped workers

Ten workers were kept in each group and 3 replications were taken at each stage of relative humidity. the average longevity of grouped workers was lowest at 33 % relative humidity (2.6 days) and highest at 100 % relative humidity (12.0 days) (Table 12). At 85 % relative humidity the average survival of workers was 7.4 days. 100 % mortality occurred after 3 days and 10 days at 33 and 85 % relative humidity respectively. At 100 % atmospheric moisture all the workers were dead within 16 days. The average longevity of insects increased slowly at 33 to 85 %, rapidly at 85 to 98 % and again slowly from 98 to 100 % relative humidity (Fig. 15).

Isolated workers

Ten isolated workers were taken at each stage of relative humidity. The minimum and maximum of the average survival of isolated workers was 1.4 and 9.8 days at 33 and 100 % relative humidity respectively. At 33 and 85 % relative humidity all

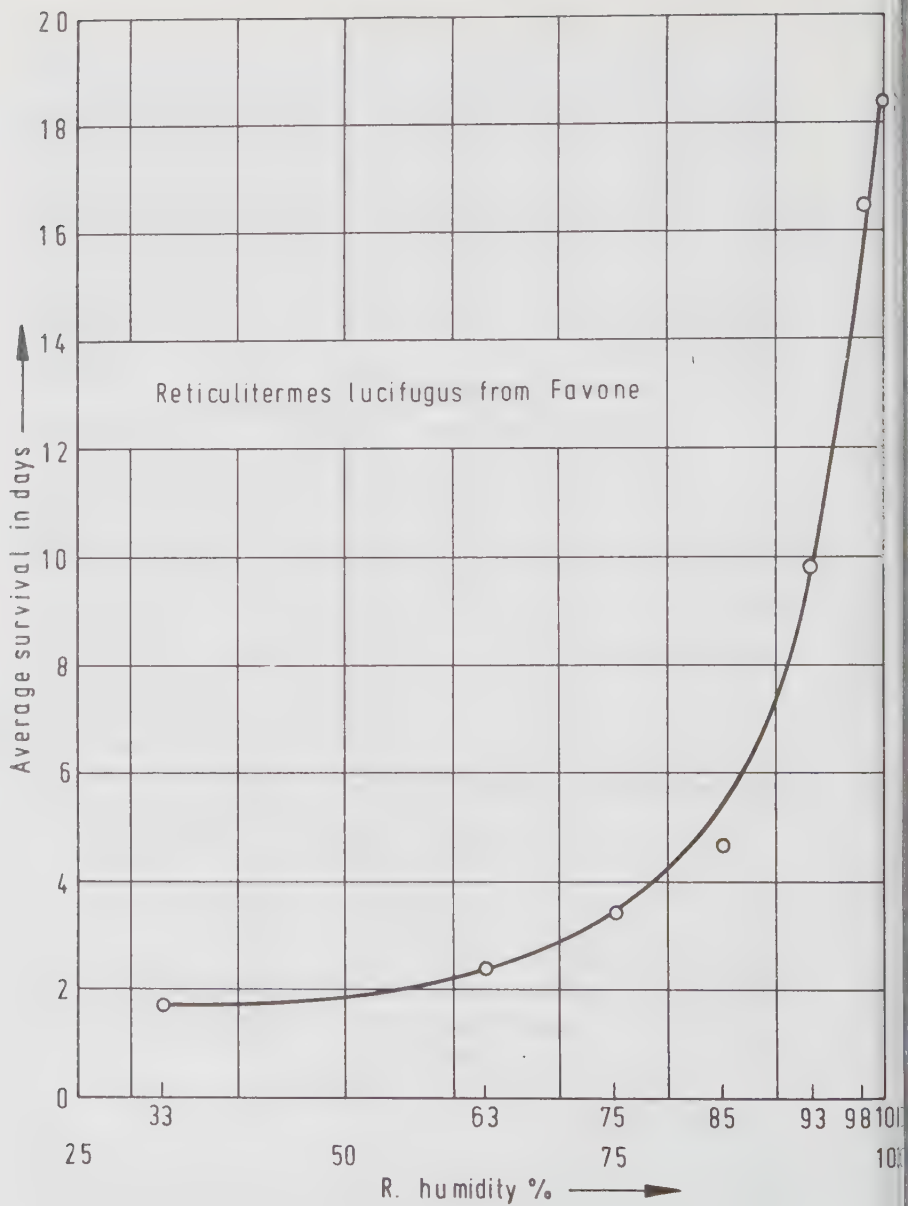


Fig. 14 - Average survival of grouped workers of *Reticulitermes lucifugus* from Favone (Corsica) under starvation conditions in relation to relative humidity at 26°C.

Table 12

Survival of workers of *Reticulitermes lucifugus* from Favone, *Reticulitermes lucifugus* from Francavilla and *Reitculitermes lucifugus* from Munich at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days									
	from Favone			from Francavilla			from Munich			
	Grouped a)		Range	Grouped a)		Range	Isolated b)		Range	Average
	Range	Average		Range	Average		Range	Average		
33	1-3	1.7	2-3	2.6	1-2	1.4	1-3	1.6	1-2	1.4
63	2-4	2.4	3-6	4.3	1-3	2.2	1-3	2.1	1-2	1.8
75	2-5	3.4	3-8	5.1	2-4	3.0	2-4	2.9	2-6	2.6
85	3-7	4.7	4-10	7.4	3-8	5.4	2-6	3.7	2-4	3.0
93	7-14	9.8	8-15	11.2	7-9	7.4	4-10	5.8	5-5	5.0
98	9-25	16.5	4-15	11.6	8-10	9.6	2-8	6.6	3-8	5.4
100	7-26	18.4	8-16	12.0	8-11	9.8	2-13	6.8	4-10	6.6

a) 10 individuals in each test group and 3 replications

b) 10 individuals kept isolated

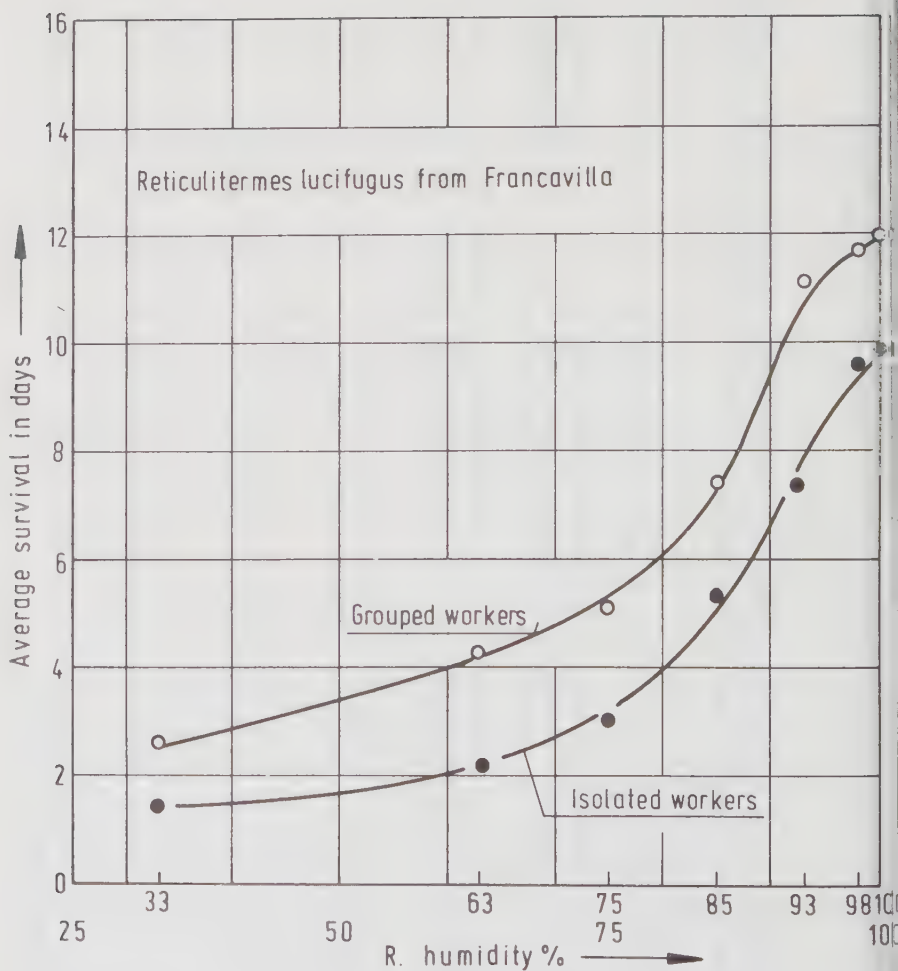


Fig. 15 - Average survival of grouped and isolated workers of *Reticulitermes lucifugus* from Francavilla under starvation conditions in relation to relative humidity at 26°C.

the isolated insects were dead within 2 and 8 days respectively. At 100 % relative humidity the last worker survived up to 11 days (Table 12). The curve of the average longevity was raised in the same way as described above for the grouped workers. Grouped workers survived slightly longer than isolated workers at all the stages of relative humidity.

3.1.1.10.3. *Reticulitermes lucifugus* from Munich

Workers of this termite were investigated in groups as well as singly at various conditions of relative humidity.

Grouped workers

Ten workers (28 mg) were taken in each group and 3 replications were provided at each stage of relative humidity. The average survival of workers was 1.6 days at 33 % and 3.7 days at 85 % relative humidity. The maximum average survival of these insects was 6.8 days at 100 % relative humidity (Table 12). At 33 and 85 % relative humidity all the workers were dead within 3 and 6 days respectively, whereas, at 100 % relative humidity the last insect was dead after 13 days.

The average longevity of insects increased more distinctly at higher percentage (85 to 100 %) of relative humidity (Fig. 16).

Isolated workers

Ten workers were kept singly at each stage of relative humidity. The minimum and maximum average survival of isolated workers was 1.4 and 6.6 days at 33 and 100 % relative humidity respectively (Table 12). 100 % mortality was observed after 2 days at 33 % relative humidity and after 10 days at 100 % relative humidity. The raising of the curve of the average longevity was the same as described above for the grouped workers (Fig. 16).

Grouped workers revealed somewhat more resistant against desiccation than isolated workers.

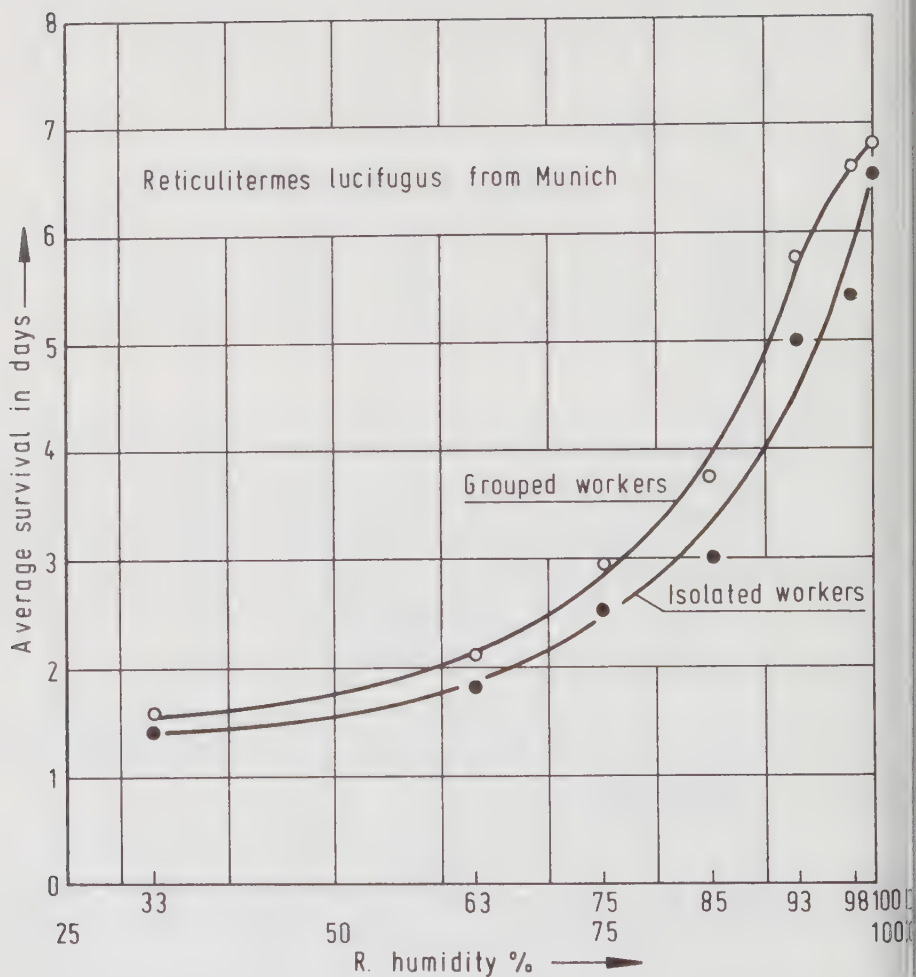


Fig. 16 - Average survival of grouped and isolated workers of *Reticulitermes lucifugus* from Munich under starvation conditions in relation to relative humidity at 26°C.

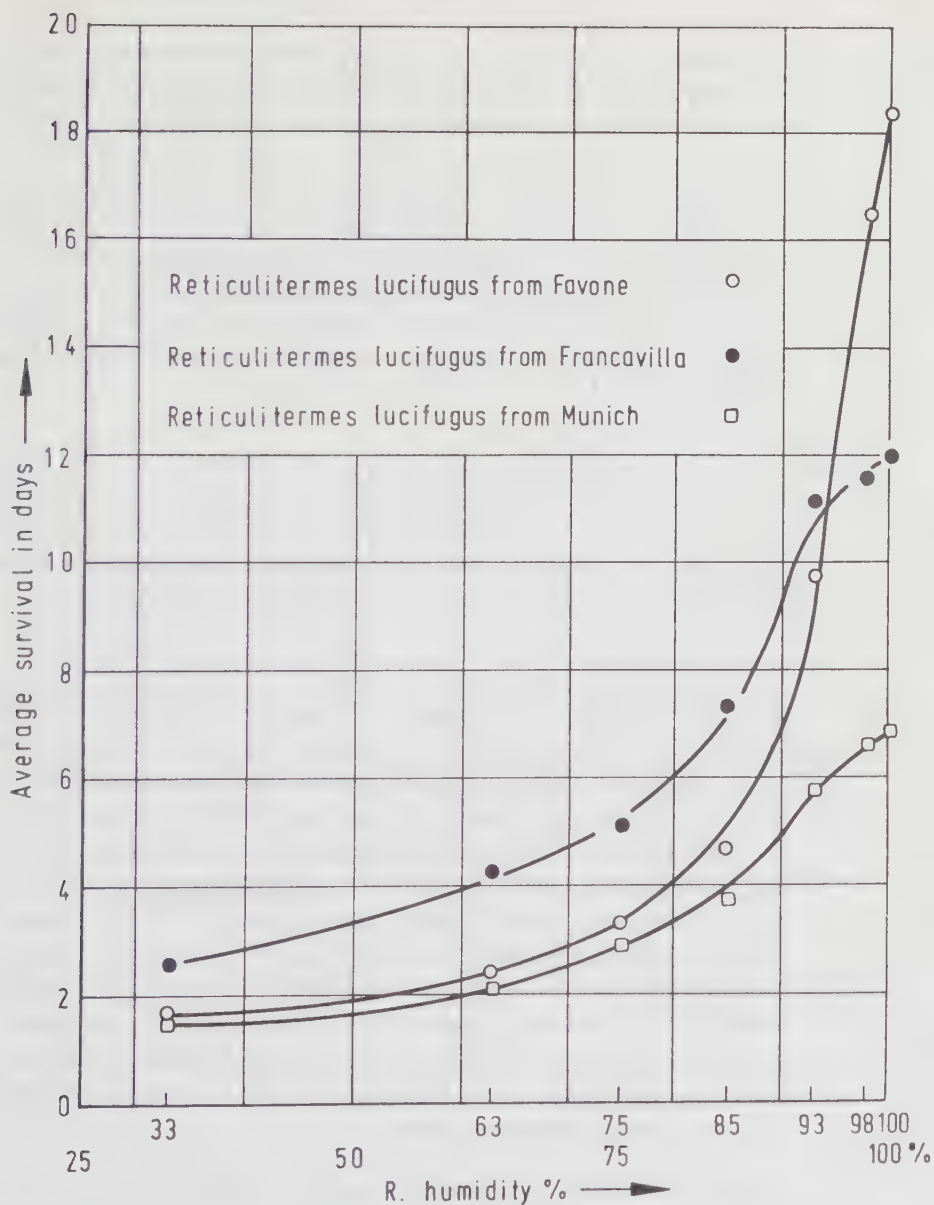


Fig. 17 - Comparison between the average survival of grouped workers of *Reticulitermes lucifugus* from Favone, Francavilla and Munich under starvation conditions in relation to relative humidity at 26°C.

A comparison between *R. lucifugus* from Francavilla, Munich and Favone showed that at lower stages of relative humidity (33 to 93 %) the termites from Francavilla showed slightly more resistance than the latter two. But above 93 % relative humidity *R. lucifugus* from Favone survived longer than *R. lucifugus* from Munich and Francavilla. At 85 to 100 % relative humidity *R. lucifugus* from Munich was more susceptible than *R. lucifugus* from Favone and Francavilla, whereas, at 33 to 85 % relative humidity *R. lucifugus* from Munich and Favone showed about the same resistance against desiccation (Fig. 17).

3.1.1.11. *Reticulitermes santonensis* Feytaud

The desiccation resistance of this species was studied with grouped and isolated workers at various conditions of relative humidity.

Grouped workers

Ten workers (28 mg) were used in each group and 3 replications were taken at each stage of relative humidity. The minimum average survival of the grouped insects was 1.9 days at 33 % relative humidity and the average survival increased with the raising of the relative humidity up to 12.6 days at 100 % relative humidity. At 33 and 85 % relative humidity 100 % mortality occurred after 2 and 7 days respectively, whereas, at 100 % relative humidity all the insects were dead within 18 days (Table 13). At lower stages (33 to 85 %) of the relative humidity the average longevity increased slowly, at higher stages of relative humidity the average longevity increased more quickly (Fig. 18). This species also showed cannibalism at 98 to 100 % relative humidity.

Isolated workers

Ten single workers were taken at each stage of relative humidity. The isolated workers showed an increasing average survival from 1.8 days at 33 % relative humidity up to 11.4 days at

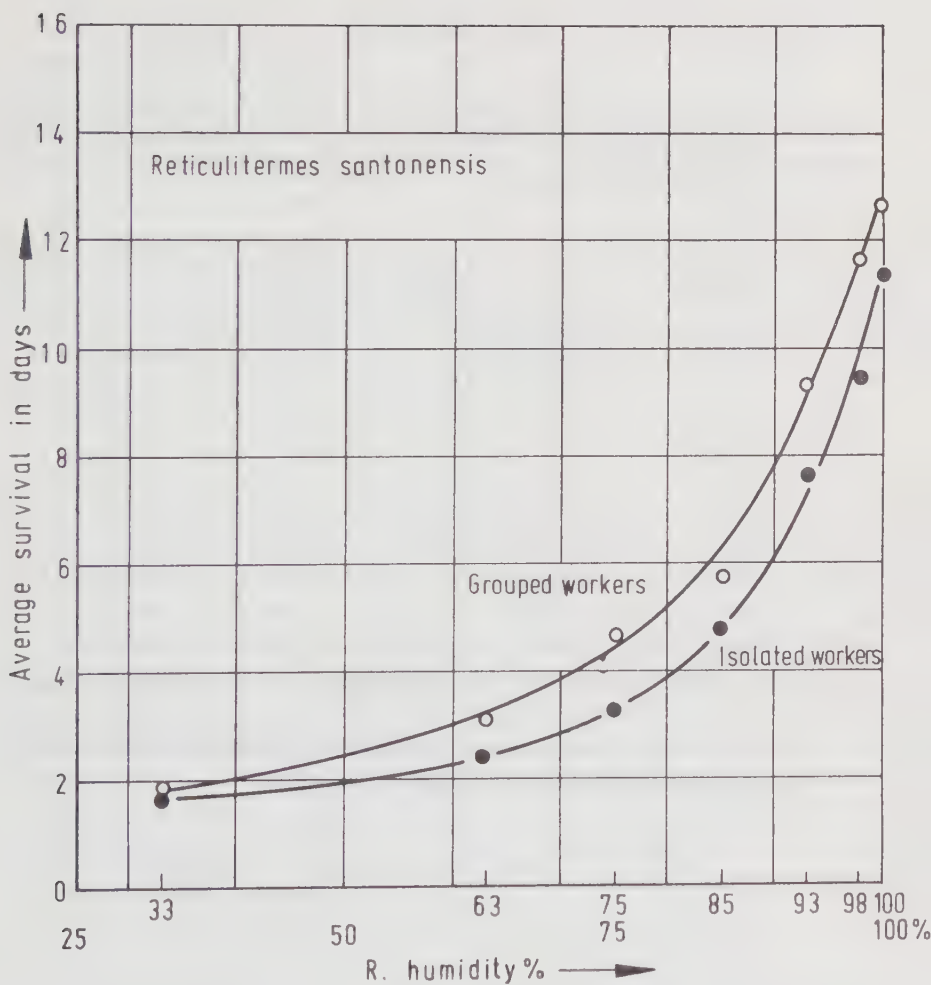


Fig. 18 - Average survival of grouped and isolated workers of *Reticulitermes santonensis* under starvation conditions in relation to relative humidity at 26°C.

Table 13

Survival of grouped and isolated workers of *Reticulitermes
santonensis* at 26°C under starvation conditions in relation
to relative humidity

Relative humidity (%)	Survival in days			
	Grouped a)		Isolated b)	
	Range	Average	Range	Average
33	1-2	1.9	1-2	1.8
63	2-4	3.0	2-3	2.4
75	3-6	4.6	3-4	3.2
85	4-7	5.7	2-6	4.8
93	6-13	9.3	6-8	7.6
98	2-15	11.6	6-13	9.4
100	8-18	12.6	8-13	11.4

a) 10 individuals in each test group and 3 replications

b) 10 individuals kept isolated

100 % relative humidity. 100 % mortality of isolated workers occurred after 2 and 13 days at 33 and 100 % relative humidity respectively (Table 13). The raising of the average longevity curve was similar to the average longevity curve of the grouped workers (Fig. 18).

The isolated workers revealed more susceptibility than the grouped workers. At 63 to 100 % relative humidity the difference in the average survival of the isolated and the grouped workers was more marked than at 33 % relative humidity.

3.1.1.12. *Reticulitermes speratus* (Kolbe) *kyushuensis* Morimoto

To study the desiccation resistance of *R. speratus kyushuensis* the workers and nymphs were used for the investigations.

Workers

Ten workers were kept in each group. The average weight of each group was about 15.2 mg and 4 replications were used at each stage of relative humidity. These studies showed that the lowest average survival of workers was 1.0 day at 33 % relative humidity which was raised slowly up to 4.0 days at 85 % relative humidity and above 85 % relative humidity the average survival increased more rapidly. However, the maximum average survival of workers was 12.0 days at 100 % relative humidity. At 33 and 85 % relative humidity 100 % mortality was observed after 2 and 6 days respectively, whereas, at 100 % relative humidity all the insects were dead within 17 days (Table 14). The curve of the average survival period raised more markedly between 85 and 100 % relative humidity than between 33 and 85 % relative humidity (Fig. 19).

Nymphs

Ten middle-sized nymphs (30.5 mg) were taken in each group and 3 replications were used at each stage of relative humidity. The minimum and maximum average survival of nymphs was 1.9 and 21.6 days at 33 and 100 % relative humidity respectively. At

Fig. 19 - Average survival of grouped workers and grouped nymphs of *Reticulitermes speratus kyushuensis* and *Reticulitermes speratus speratus* under starvation conditions in relation to relative humidity at 26°C.

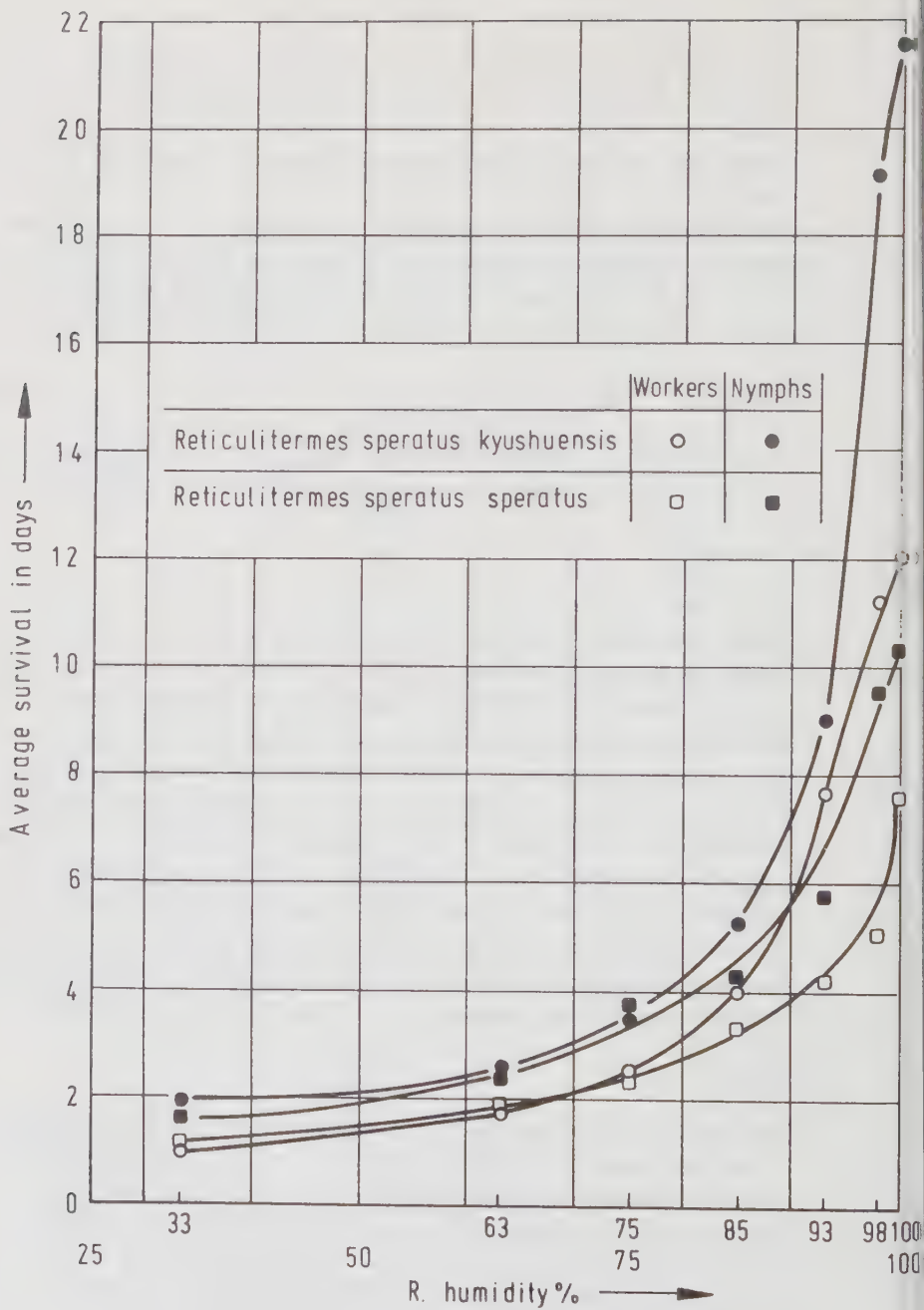


Fig. 19

Table 14

Survival of grouped workers and grouped nymphs of *Reticulitermes speratus kyushuensis* and *Reticulitermes speratus* at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	R. speratus kyushuensis				R. speratus speratus			
	Workers a)		Nymphs b)		Workers b)		Nymphs b)	
	Range	Average	Range	Average	Range	Average	Range	Average
33	1-2	1.0	1-2	1.9	1-2	1.2	1-2	1.7
63	1-2	1.8	2-3	2.6	1-2	1.9	1-4	2.4
75	2-3	2.5	3-4	3.5	2-4	2.4	2-4	3.7
85	3-6	4.0	4-6	5.3	2-5	3.3	4-6	4.2
93	6-10	7.7	6-10	9.0	2-6	4.1	4-8	5.8
98	6-15	11.3	17-24	19.1	2-8	5.0	6-11	9.5
100	6-17	12.0	13-34	21.6	4-11	7.6	4-13	10.3

a) 10 individuals in each group and 4 replications

b) 10 individuals in each group and 3 replications

85 % relative humidity the average survival of nymphs was 5.3 days (Table 14). At 33 and 85 % relative humidity all the nymphs were dead after 2 and 6 days respectively. But at 100 % relative humidity 100 % mortality was observed after 34 days. The average longevity of nymphs increased very slowly from 33 to 85 % relative humidity, whereas, at 85 to 100 % relative humidity the average survival increased very rapidly (Fig. 19).

Nymphs proved more resistant against desiccation than workers. But the difference in the average survival was more distinct from 93 to 100 % relative humidity.

3.1.1.13. *Reticulitermes speratus* (Kolbe) *speratus* Morimoto

Workers and nymphs of this termite were tested under starvation conditions in relation to relative humidity.

Workers

Ten workers (20.5 mg) were taken in each group and 3 replications were used at each stage of relative humidity. The average survival of workers was 1.2 days at 33 % relative humidity which was increased slowly up to 5.0 days at 98 % relative humidity. But the maximum average survival of workers was 7.6 days at 100 % relative humidity (Table 14). 100 % mortality was observed after 2, 5 and 11 days at 33, 85 and 100 % relative humidity respectively. The average survival curve raised gradually from 33 to 98 % and rapidly from 98 to 100 % relative humidity (Fig. 19).

Nymphs

Ten middle-sized nymphs (38.6 mg) were selected for each group with 3 replications at each stage of relative humidity. Nymphs showed the minimum average survival of 1.6 days at 33 % relative humidity. The average survival was increased slowly up to 4.2 days at 85 % relative humidity. But from 85 to 100 % relative humidity the average longevity of nymphs increased

very rapidly, e.g. 10.3 days at 100 % relative humidity. 100 % mortality was observed after 2, 6 and 13 days at 33, 85 and 100 % relative humidity respectively.

As shown in Fig. 19 the curve of the average longevity raised gradually from 33 to 93 % relative humidity but between 93 and 100 % relative humidity the curve of the average longevity raised more distinctly.

Workers were more susceptible than nymphs during drying. But the difference was more distinct between 85 and 100 % relative humidity than between 33 and 85 % relative humidity.

3.1.1.14. *Reticulitermes tibialis* Banks

Ten workers with an average weight of 25.5 mg were kept in each group and 3 replications were used at each stage of relative humidity.

Workers showed a lowest average survival of 3.1 days at 33 % relative humidity and a maximum average survival of 24.0 days at 100 % relative humidity. The average longevity of workers was 6.9 days at 85 % relative humidity. At 33 and 85 % relative humidity all the workers were dead within 4 and 9 days respectively. The highest survival period of workers was 35 days at 100 % relative humidity (Table 11). As shown in Fig. 13, the average longevity of animals increased gradually between 33 and 85 % relative humidity, whereas, from 85 to 100 % the average longevity increased very distinctly.

At 100 % relative humidity 50 and 90 % mortality was observed after 22 and 33 days respectively. *R. tibialis* required a high and narrow range of relative humidity (100 %). Thus, it may be called a stenohygrous species.

3.1.1.15. *Reticulitermes virginicus* (Banks)

In the case of *R. virginicus* the experiments were done with workers (grouped and isolated) and nymphs (grouped and isolated) at different stages of relative humidity.

Grouped workers

Ten individuals were selected in each group, the average weight of each group was 22.5 mg and 3 replications were taken at each stage of relative humidity.

The workers showed an increase in the average longevity from 1.8 days at 33 %, 4.9 days at 85 % up to 11.1 days at 100 % relative humidity. 100 % mortality was observed after 2 and 7 days at 33 and 85 % relative humidity respectively. At 100 % relative humidity all the insects were dead after 14 days (Table 15).

Average longevity (Fig. 20) increased slowly from 33 to 85 % and rapidly from 85 to 100 % relative humidity.

Isolated workers

Ten isolated workers were used at each stage of relative humidity. The lowest and highest average survival of isolated workers was 1.6 and 9.2 days at 33 and 100 % relative humidity respectively. At 33, 85 and 100 % relative humidity the longest survival of single workers was about the same as the highest survival of grouped workers (Table 15).

Grouped workers showed more resistance against drying than single workers. But the difference in the average survival was more distinct at 100 % relative humidity than at 33 to 98 % relative humidity.

Grouped nymphs

Five nymphs (16.5 mg) were kept in each group with 3 replications at each stage of the relative humidity. Nymphs showed the lowest average survival of 2.0 days at 33 % relative humidity which was increased gradually up to 7.6 days at 93 % relative humidity. But above 93 % relative humidity the survival period of nymphs increased very quickly. The maximum average survival of nymphs was 16.5 days at 100 % relative humidity (Table 15). All the nymphs were dead after 3 and 9 days

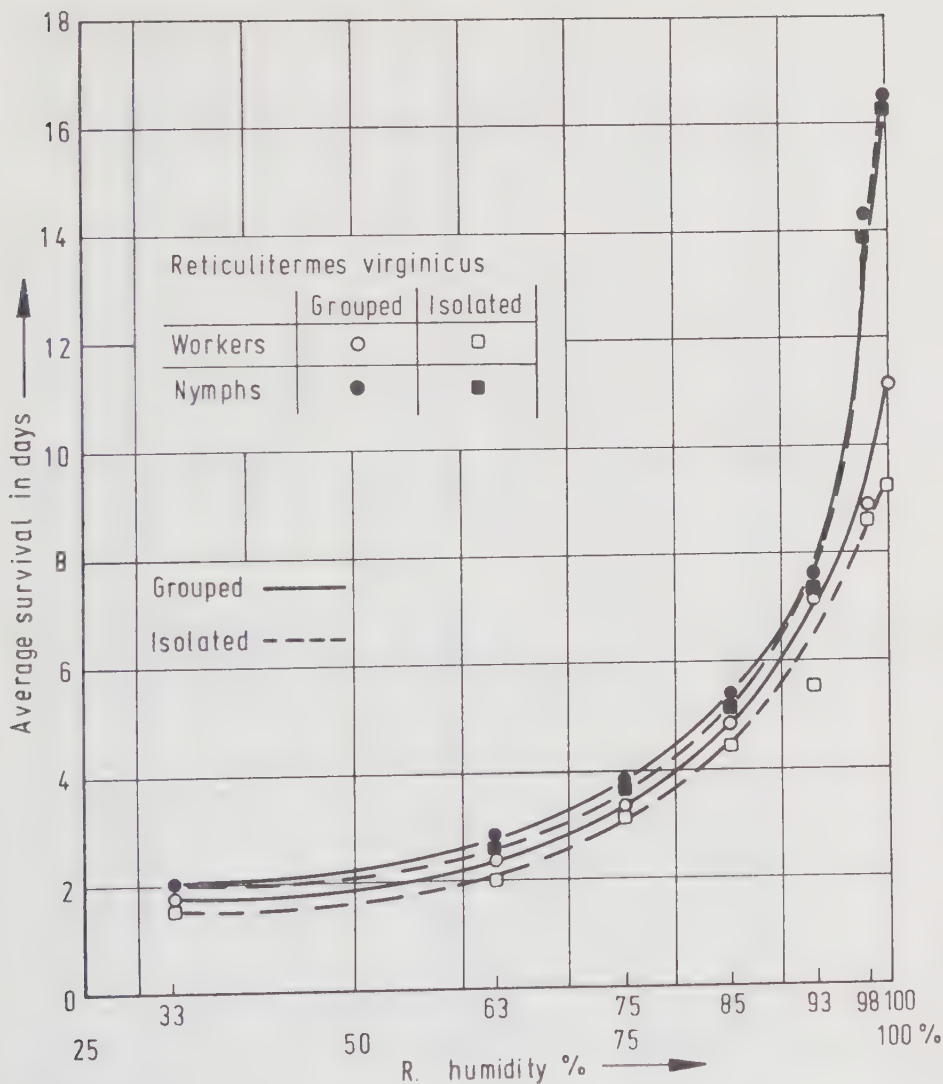


Fig. 20 - Average survival of workers (grouped and isolated) and nymphs (grouped and isolated) of *Reticulitermes virginicus* under starvation conditions in relation to relative humidity at 26°C.

Table 15

Survival of workers (grouped and isolated) and nymphs (grouped and isolated) of *Reti-
culitermes virginicus* at 26°C under starvation conditions in relation to relative humi-
dity

Relative humidity (%)	Survival in days							
	Workers				Nymphs			
	Grouped a)		Isolated b)		Grouped c)		Isolated d)	
	Range	Average	Range	Average	Range	Average	Range	Average
33	1-2	1.8	1-2	1.6	1-3	2.0	1-3	2.0
63	2-3	2.4	2-2	2.0	2-3	2.9	2-3	2.4
75	2-6	3.4	3-4	3.2	3-5	3.8	3-4	3.6
85	3-7	4.9	3-7	4.4	4-7	5.4	4-7	5.1
93	2-9	7.2	2-7	5.5	7-9	7.6	2-11	7.2
98	2-11	8.9	7-11	8.6	11-18	14.3	11-16	13.8
100	7-14	11.1	2-14	9.2	14-21	16.5	7-21	16.4

a) 10 individuals in each test group and 3 replications

b) 10 individuals kept isolated

c) 5 individuals in each test group and 3 replications

d) 5 individuals kept isolated

at 33 and 93 % relative humidity respectively, whereas, at 100 % relative humidity the last nymph survived up to 21 days. The curve of the average survival raised slowly from 33 to 93 % and very rapidly from 93 to 100 % relative humidity (Fig. 20). Nymphs didn't show any cannibalism during the tests.

Isolated nymphs

Five isolated nymphs were provided at every stage of relative humidity. The lowest average survival of isolated nymphs was 2.0 days at 33 % relative humidity, which was increased slowly up to 7.2 days at 93 % relative humidity, but between 93 and 100 % relative humidity average survival increased very markedly. The maximum average survival of isolated nymphs was 16.4 days at 100 % relative humidity (Table 15). The highest survival of isolated nymphs was about the same as the highest survival of grouped nymphs.

Isolated nymphs showed about the same resistance against drying as grouped nymphs at all stages of relative humidity of the air (Fig. 20). 100 % relative humidity proved the optimum for the survival of workers and nymphs.

A comparison between the desiccation resistance of nymphs and workers showed that at 33 to 93 % relative humidity nymphs were slightly more resistant than workers. But between 93 and 100 % relative humidity the survival period of nymphs increased more rapidly than the survival period of workers.

3.1.1.16. *Prorethra simplex* (Hagen)

Ten workers (23.5 mg) were kept in each group and 3 replications were taken at each stage of relative humidity.

The lowest average survival of workers was 2.7 days at 33 % relative humidity, which increased with the raising of relative humidity. However, the maximum average survival of *P. simplex* increased up to 15.9 days at 100 % relative humidity (Table 16). 100 % mortality was observed after 4 and 11 days at 33 and 85 %

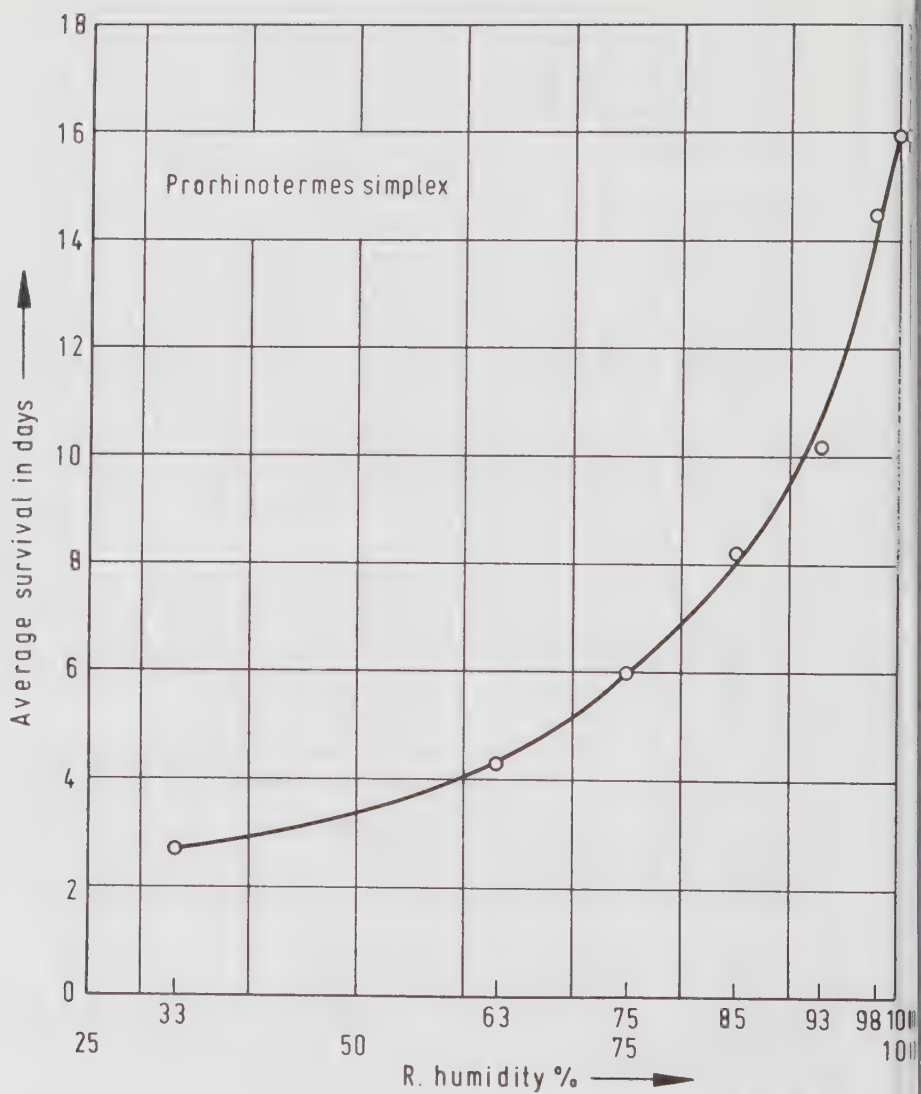


Fig. 21 - Average survival of grouped workers of *Prorhinotermes simplex* under starvation conditions in relation to relative humidity at 26°C.

Table 16

Survival of workers of Prothino-
termes simplex at 26°C under star-
vation conditions in relation to
relative humidity

Relative humidity	Survival in days	
	Range	Average
33	1-4	2.7
63	4-7	4.3
75	4-7	6.0
85	7-11	8.2
93	7-13	10.2
98	7-18	14.4
100	9-23	15.9

10 individuals in each test group
and 3 replications

Table 17

Survival of workers and soldiers of Microcero-
termes championii at 26°C under starvation con-
ditions in relation to relative humidity

Relative humidity	Survival in days			
	Workers a)		Soldiers b)	
(%)	Range	Average	Range	Average
33	1-3	2.5	1-2	1.4
63	1-7	3.9	1-3	2.2
75	3-9	5.9	3-4	3.1
85	4-12	7.1	2-5	4.1
93	3-21	10.0	3-9	5.8
98	4-42	15.6	4-15	8.4
100	5-46	18.9	4-19	10.8

a) 20 individuals in each test group and 5 replications

b) 5 individuals in each test group and 3 replications

relative humidity respectively, whereas, at 100 % relative humidity all the workers died within 23 days. Between 33 and 85 % relative humidity the curve of the average survival increased gradually (Fig. 21). But between 85 and 100 % relative humidity the average longevity curve increased more strongly. 100 % atmospheric moisture proved the most suitable for *P. simplex*.

3.1.1.17 *Microcerotermes championi* Snyder

In the case of *M. championi* the investigations were carried out with grouped workers and grouped soldiers.

Workers

Twenty workers (38 mg) in each group and 5 replications were taken at each stage of relative humidity.

The lowest average survival period of workers was 2.5 days at 33 % relative humidity. The average survival increased slowly up to 7.1 days at 85 % relative humidity. But above 85 % relative humidity the insects showed a very rapid increase in the average longevity. The maximum average longevity of workers was 18.9 days at 100 % relative humidity. At 33 and 85 % relative humidity 100 % mortality was observed after 3 and 12 days respectively. But at 100 % relative humidity the last worker survived up to 46 days (Table 17). As shown in Fig. 22 the average survival curve raised slowly from 33 to 85 % relative humidity, whereas, between 85 and 100 % relative humidity the average survival curve raised very strongly.

Soldiers

Five soldiers (9.5 mg) were taken in each group and 3 replications were used at each stage of relative humidity.

The average survival of soldiers was increased slowly from 1.4 days (33 % relative humidity) up to 4.1 days (85 % relative humidity). Above 85 % relative humidity the average longe-

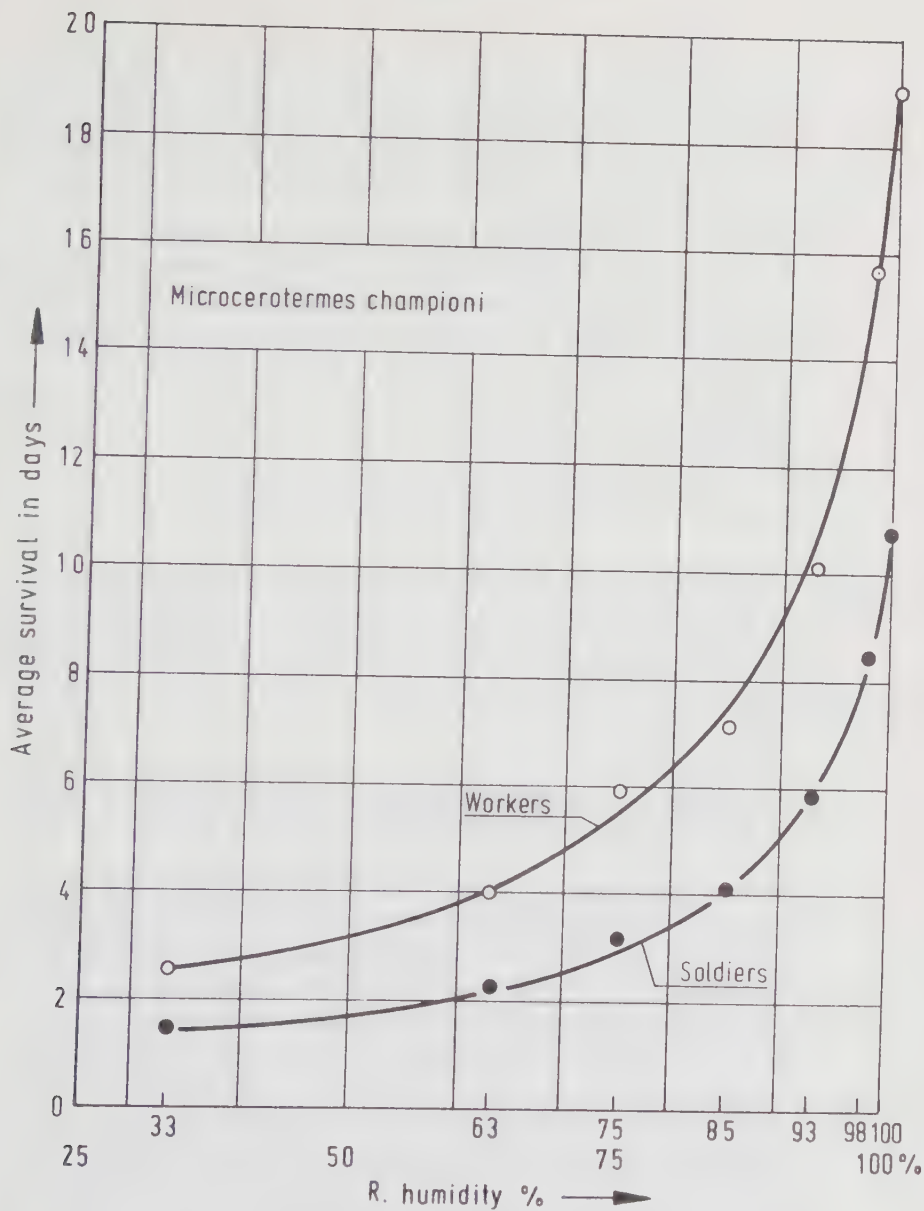


Fig. 22 - Average survival of grouped workers and grouped soldiers of *Microcerotermes championi* under starvation conditions in relation to relative humidity at 26°C.

vity of soldiers increased up to 10.8 days at 100 % relative humidity (Table 17). At 33 and 85 % relative humidity the longest survival of soldiers was 2 and 5 days respectively. But the last soldier of *M. championi* survived up to 19 days at 100 % relative humidity. The average longevity curve raised in the same way as described for the workers. Workers revealed more resistance against drying than soldiers. At higher stages of relative humidity the survival period of workers increased more rapidly than the survival period of soldiers. 100 % relative humidity is the optimum for the workers and soldiers of *M. championi*.

3.1.1.18. *Microcerotermes crassus* Snyder

In the case of *M. crassus* investigations were carried out with workers (grouped and isolated) and soldiers (grouped and isolated) under starvation conditions at different stages of relative humidity.

Grouped workers

Ten workers (22 mg) were taken in each group and 3 replications were used at each stage of relative humidity.

Grouped workers showed the lowest average survival of 4.0 days (33 % relative humidity) which was increased slowly up to 10.4 days at 85 % relative humidity. But above 85 % relative humidity the survival period of insects increased very rapidly. The maximum average survival of workers was 20.3 days at 100 % relative humidity (Table 18). 100 % mortality was observed after 7 and 18 days at 33 and 85 % relative humidity respectively. But at 100 % relative humidity all the insects were dead within 35 days. Between 33 and 85 % relative humidity the curve of the average longevity raised slowly, whereas, between 85 and 100 % relative humidity the curve of the average longevity raised very strongly (Fig. 23).

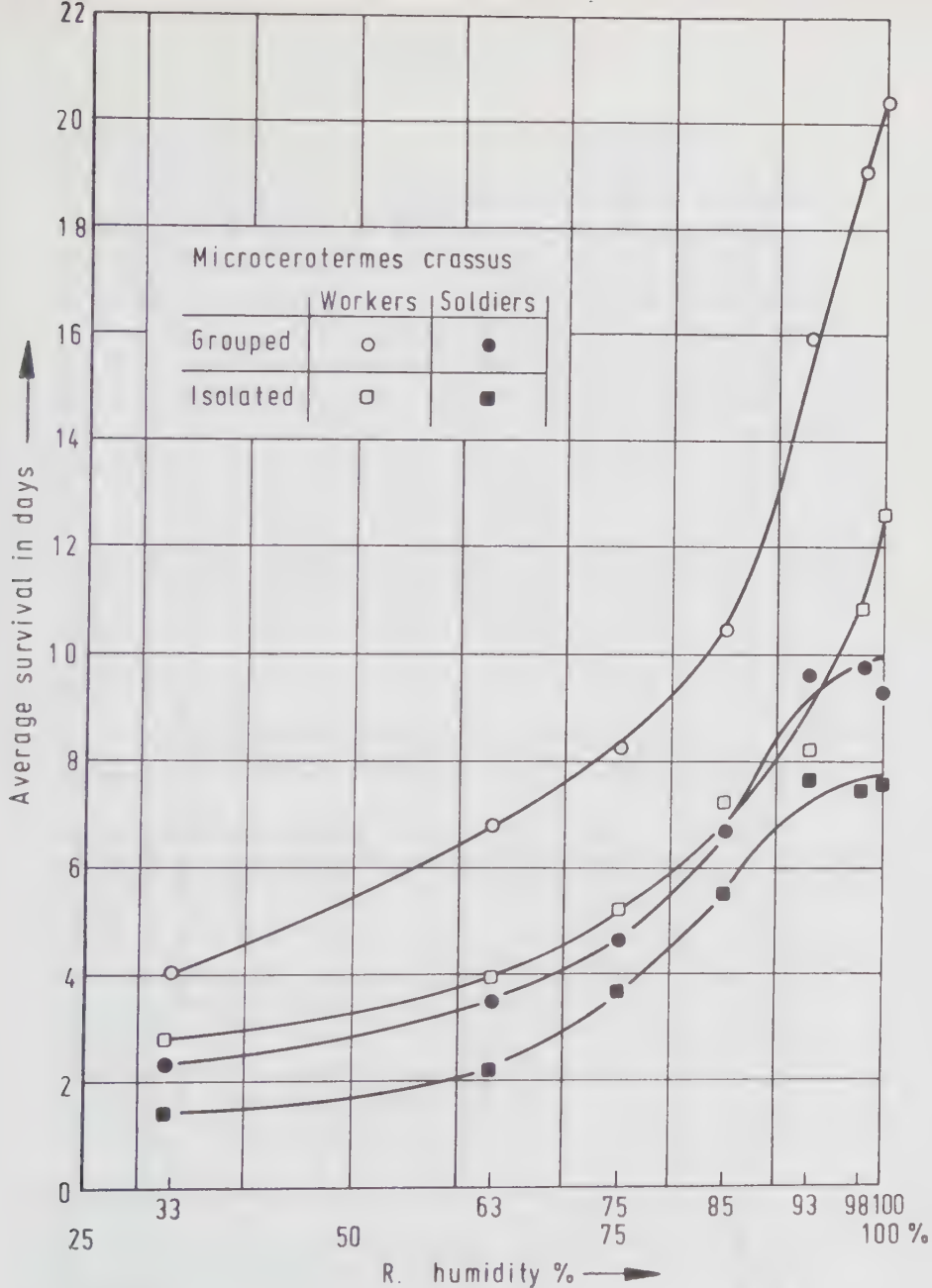


Fig. 23 - Average survival of workers (grouped and isolated) and soldiers (grouped and isolated) of *Microcerotermes crassus* under starvation conditions in relation to relative humidity at 26°C.

Table 18

Survival of workers (grouped and isolated) and soldiers (grouped and isolated) of *Microcerotermes crassus* at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days							
	Workers				Soldiers			
	Grouped a)		Isolated b)		Grouped c)		Isolated b)	
	Range	Average	Range	Average	Range	Average	Range	Average
33	2-7	4.0	2-4	2.8	1-3	2.3	1-2	1.4
63	3-9	6.8	2-7	3.9	1-5	3.5	1-3	2.2
75	3-11	8.2	3-10	5.2	2-9	4.6	3-7	3.7
85	7-18	10.4	4-10	7.2	2-12	6.6	3-10	5.5
93	7-28	15.9	3-14	8.2	3-19	9.7	4-10	7.7
98	2-31	19.1	4-23	10.9	4-15	9.8	4-10	7.3
100	9-35	20.3	4-25	12.6	4-16	9.2	4-12	7.6

a) 10 individuals in each test group and 3 replications

b) 10 individuals kept isolated

c) 10 individuals in each test group and 4 replications

Isolated workers

Ten isolated workers were used at each stage of relative humidity. The shortest and longest time of average survival of isolated workers was 2.8 and 12.6 days at 33 and 100 % relative humidity respectively. At 33 and 85 % relative humidity all the insects were dead within 4 and 10 days respectively. But at 100 % relative humidity the last isolated worker survived up to 25 days (Table 18). The curve of the average longevity raised more markedly at 93 to 100 % relative humidity than at 33 to 93 % (Fig. 23).

Grouped workers were more resistant against desiccation than isolated ones. The difference in the survival time of grouped and isolated workers increased with raising relative humidity of the air.

Grouped soldiers

Ten soldiers (21.5 mg) were kept in each group and 4 replications were taken at each stage of relative humidity.

Grouped soldiers showed the lowest average survival time of 2.3 days at 33 % relative humidity. The time increased slowly up to 4.6 days at 75 % relative humidity. From 75 to 93 % relative humidity the average survival increased rapidly (e.g. 9.7 days at 93 % relative humidity). From 93 to 100 % relative humidity soldiers revealed about the same survival period. At 33 and 75 % relative humidity all the soldiers were dead within 3 and 9 days respectively. But the last insect survived up to 19 days at 93 % relative humidity (Table 18).

Isolated soldiers

Ten isolated soldiers were taken at each stage of relative humidity.

Isolated soldiers showed the lowest average survival of 1.4 days at 33 % relative humidity. The average survival time of

isolated soldiers increased slowly up to 3.7 days at 75 % relative humidity (Fig. 23). Between 75 and 93 % relative humidity the average longevity of soldiers increased rapidly (e.g. 7.7 days at 93 % relative humidity). From 93 to 100 % relative humidity the insects showed about the same average survival. At 33 and 75 % relative humidity all the soldiers were dead within 2 and 7 days respectively. But the highest survival of the isolated soldiers was 12 days at 100 % relative humidity ((Table 18). The average longevity curve raised in the same way as described above for the grouped soldiers. Grouped soldiers showed more longevity than isolated soldiers under desiccation conditions.

Workers showed more resistance against desiccation than soldiers and the difference in the desiccation resistance of workers and soldiers increased with raising relative humidity of the air.

The difference in the survival period of grouped and isolated workers was more than the difference in the survival period of grouped and isolated soldiers.

These studies also revealed that the difference in the survival period of grouped workers and grouped soldiers was more than the difference in the survival period of isolated workers and isolated soldiers.

100 % relative humidity is the optimum for the workers of *M. crassus*. But the soldiers showed about the same survival period at 93 to 100 % relative humidity.

3.1.1.19. *Nasutitermes nigriceps* (Haldeman)

Workers and soldiers of *N. nigriceps* were tested in following group compositions: grouped workers, grouped soldiers, isolated workers, isolated soldiers, heterogenous groups (workers and soldiers grouped together).

Grouped workers

Twenty workers were taken in each group and 5 replications were provided at each stage of relative humidity. The average weight of each group was about 118 mg.

At 33 % relative humidity the insects showed an average survival of 2.9 days which raised slowly up to 6.0 days at 85 % relative humidity. But above 85 % relative humidity the survival period of insects increased markedly and at 100 % relative humidity the animals showed the maximum average longevity of 15.2 days (Table 19). At 33, 85 and 100 % atmospheric moisture all the workers were dead within 3, 10 and 23 days respectively. The increase of the average longevity curve was slow at lower atmospheric moisture (33 to 85 %) but at higher atmospheric moisture (85 to 100 %) the curve of the average longevity was raised rapidly (Fig. 24).

Isolated workers

Ten isolated workers were provided at each stage of atmospheric moisture.

The minimum and maximum average survival period of isolated workers was 1.8 and 6.2 days at 33 and 100 % atmospheric moisture respectively. All the single workers were dead after 2 days at 33 % relative humidity, after 5 days at 75 and 85 % relative humidity (Table 19) and after 12 days at 100 % relative humidity. The average longevity curve raised slowly from 33 to 85 % relative humidity, rapidly from 85 to 98 % relative humidity and again slowly from 98 to 100 % relative humidity (Fig. 24).

Grouped workers showed longer average survival than isolated workers. At higher stages of the atmospheric moisture the average survival of grouped workers increased more strongly than the average survival of isolated workers.

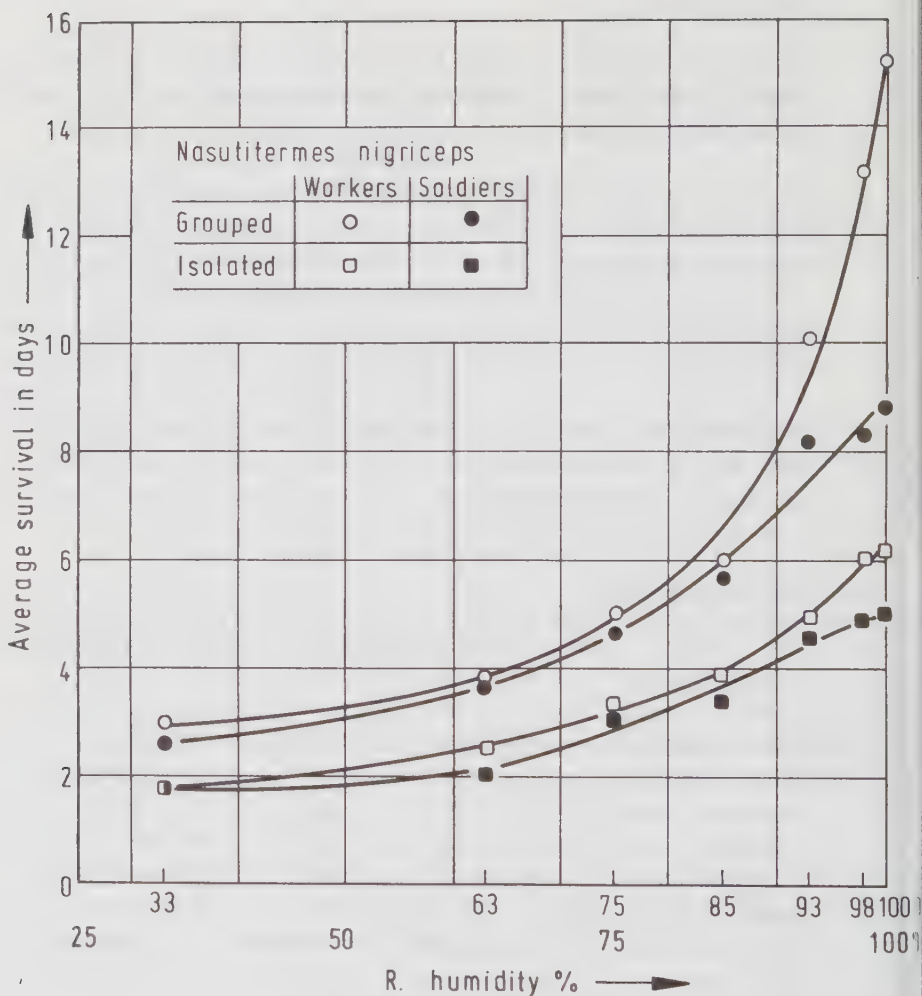


Fig. 24 - Average survival of workers (grouped and isolated) and soldiers (grouped and isolated) of *Nasutitermes nigriceps* under starvation conditions in relation to relative humidity at 26°C.

Table 19

Survival of workers (grouped and isolated) and soldiers (grouped and isolated) of *Nasutitermes nigricipes* at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days					
	Workers			Soldiers		
	Grouped a) Range	Average	Isolated b) Range	Grouped a) Range	Average	Isolated b) Range
33	1-3	2.9	1-2	1-4	2.6	1-2
63	3-5	3.9	1-4	2-5	3.8	1-3
75	3-8	5.0	2-5	2-7	4.7	2-4
85	2-10	6.0	2-5	2-8	5.6	2-5
93	6-14	10.1	2-6	3-12	8.2	2-6
98	4-22	13.2	3-11	3-13	8.2	2-7
100	3-23	15.2	3-12	3-11	8.8	2-9

a) 20 individuals in each test group and 5 replications

b) 10 individuals kept isolated

Grouped soldiers

Twenty soldiers (48 mg) were kept in each group and 5 replications were used at each stage of relative humidity.

Grouped soldiers showed an increase in the average survival from 2.6 days at 33 %, 5.6 days at 85 % up to 8.8 days at 100 % relative humidity. All the soldiers were dead within 4 days at 33 % relative humidity, within 8 days at 85 % relative humidity and within 13 days at 98 % relative humidity (Table 19). The curve of average longevity raised slowly from 33 to 85 % relative humidity, rapidly from 85 to 93 % and again slowly from 93 to 100 % relative humidity (Fig. 24).

Isolated soldiers

Ten isolated soldiers were taken at each stage of relative humidity.

Isolated soldiers showed a lowest average survival of 1.8 days at 33 % relative humidity. With the increase of relative humidity the average survival of soldiers increased slowly. The maximum average survival of soldiers was 5.0 days at 100 % relative humidity. At 33 and 100 % relative humidity all the isolated soldiers were dead within 2 and 9 days respectively (Table 19). The curve of the average survival was raised gradually from 33 to 100 % relative humidity (Fig. 24).

Grouped soldiers showed more resistance against desiccation than isolated soldiers and the difference in the desiccation resistance of grouped and isolated soldiers was more distinct at 85 to 100 % relative humidity than at 33 to 85 % relative humidity.

At 33 to 93 % relative humidity isolated soldiers and isolated workers showed about the same survival period but from 93 to 100 % relative humidity isolated workers survived somewhat longer than isolated soldiers.

At 33 to 85 % relative humidity the grouped workers and grouped soldiers did not show any difference in the average longevity, whereas, between 85 and 100 % relative humidity the average longevity of workers increased more strongly than the average longevity of soldiers

At higher stages of relative humidity (85 to 100 %) the difference between the survival period of grouped workers and grouped soldiers was more than the difference between the survival period of isolated workers and isolated soldiers.

At higher stages of atmospheric moisture the difference between the survival period of grouped and isolated workers was more than the difference between the survival period of grouped and isolated soldiers.

Heterogenous groups

Twenty workers and 10 soldiers were kept together in each group and 5 replications were supplied at each stage of relative humidity.

Workers

The lowest and highest average survival of workers was 2.9 and 12.7 days at 33 and 100 % relative humidity respectively. The last worker was dead after 20 days at 98 % relative humidity (Table 20).

The curve of the average survival of workers increased slowly from 33 to 85 % relative humidity and rapidly from 85 to 100 % relative humidity (Fig. 25).

Soldiers

The minimum and maximum average survival of soldiers was 3.2 and 12.8 days at 33 and 100 % relative humidity respectively. The last soldier (in heterogenous groups) was dead after 22 days at 98 % relative humidity (Table 20). The curve of the

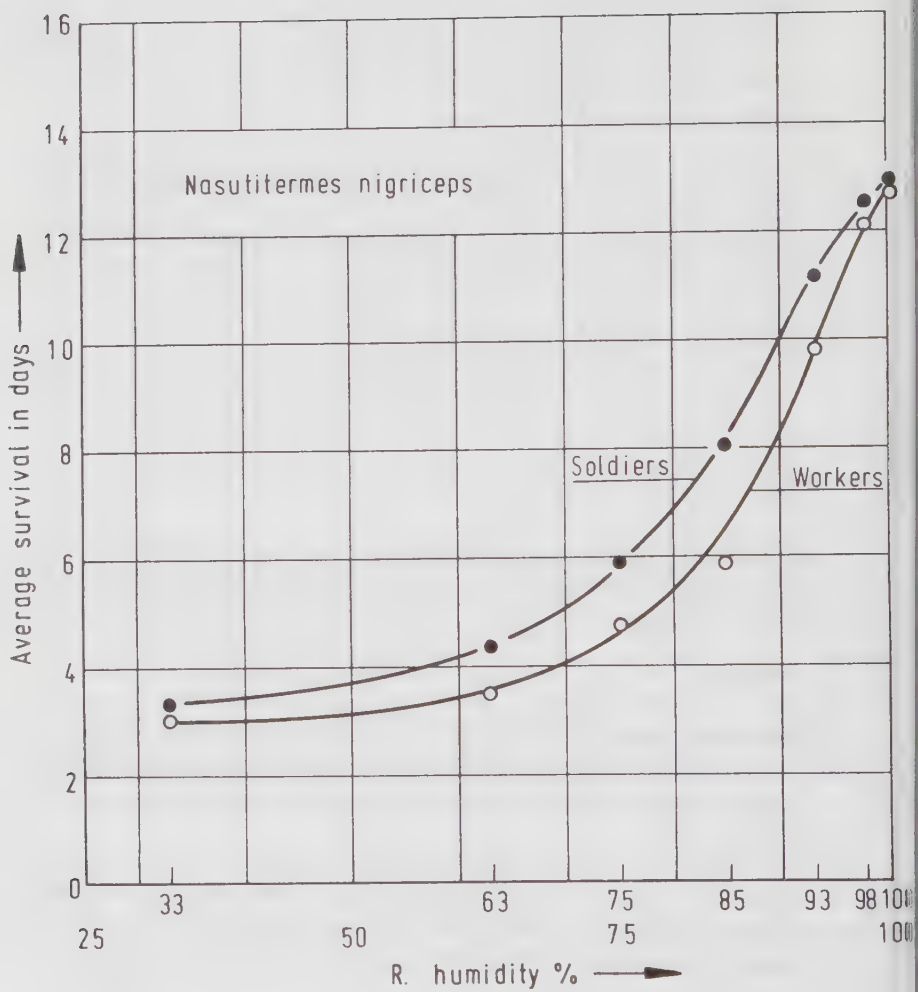


Fig. 25 - Average survival of workers and soldiers of *Nasutitermes nigriceps* under starvation conditions in relation to relative humidity at 26°C when kept in heterogenous groups (20 workers and 10 soldiers in each group).

Table 20

Survival of workers and soldiers of *Nasutitermes nigriceps* kept in heterogenous groups (20 workers and 10 soldiers together in each test group) at 26°C under starvation conditions in relation to relative humidity

Relative humidity (%)	Survival in days			
	Workers		Soldiers	
	Range	Average	Range	Average
33	1-4	2.9	1-4	3.2
63	3-6	3.5	3-6	4.4
75	3-8	4.7	4-10	5.9
85	5-14	5.9	6-16	8.1
93	7-18	9.8	8-20	11.1
98	5-20	12.1	6-22	12.5
100	4-18	12.7	7-20	12.8

5 replications at each stage of relative humidity

average longevity was raised in the same way as described above for the workers (Fig. 25).

In heterogenous groups, soldiers revealed somewhat longer survival period than the survival period of workers at all the stages of relative humidity.

Soldiers in heterogenous groups survived longer (Table 20) under desiccation conditions than homogenous groups of soldiers (Table 19).

Workers in heterogenous groups survived shorter under desiccation conditions than homogenous groups of workers.

3.1.2. Comparison of the results

3.1.2.1. Comparison between workers or pseudergates of various species of termites

These experiments proved (Table 21) that the highest relative humidity (100 %) was optimum for Rhinotermitidae, Termopsidae and Termitidae species, but fatal for Kalotermitidae species. On the other hand, dry-wood termites were resistant to lower atmospheric moisture, whereas, damp-wood termites, subterranean termites and nest-building termites proved very susceptible to a lower relative humidity of air.

Of the Kalotermitidae species, *Cryptotermes dudleyi* and *Kalotermes flavicollis* revealed the highest resistance against dry conditions compared with other termite species. The longest period of survival of pseudergates of *Neotermes jouteli* was 64 days at 98 %, of *K. flavicollis* 129 days at 85 % and of *C. dudleyi* 114 days at 63 % relative humidity.

The optimum range of relative humidity for *N. jouteli* was 90 to 99 %, for *K. flavicollis* 80 to 95 % and *C. dudleyi* showed the highest average survival at 33 to 85 % relative humidity. The average survival of *N. jouteli* was about 50 % of that of *K. flavicollis* and *C. dudleyi*. In succession as follows *N. jouteli*, *K. flavicollis* and *C. dudleyi* species preferred a lower atmospheric moisture.

N. jouteli was slightly more resistant at a lower atmospheric moisture (33 - 63 %) than *Zootermopsis angusticollis*, whereas, the latter termite survived longer at higher atmospheric moisture. *Z. angusticollis* (Termopsidae) required a higher atmospheric moisture than the Kalotermitidae species. But *Z. angusticollis* (highest body weight of pseudergates compared with all the species of termites tested) showed a greater resistance to desiccation than Rhinotermitidae and Termitidae species.

The difference in the susceptibility of Rhinotermitidae and Termitidae species was very small at lower atmospheric moisture. But these species revealed higher differences in resistance at higher relative humidities. *Heterotermes indicola* (lowest body weight of workers in comparison with all species of termites tested) proved to be more resistant to drying than *Coptotermes*, *Reticulitermes*, *Prorhinotermes* (Rhinotermitidae), *Microcerotermes* and *Nasutitermes* (Termitidae) species. Moreover, *H. indicola* cultured at 30°C survived slightly longer than those cultured at 26°C under desiccation conditions

H. indicola was followed by *Reticulitermes tibialis*, showing an average survival of 24 days at 100 % relative humidity. *R. tibialis* and *R. hesperus* showed about the same resistance at lower atmospheric moisture, whereas, at the highest relative humidity *R. tibialis* proved more resistant to starving than *R. hesperus*.

In the succession of decreasing resistance to desiccation the above cited species were followed by *Microcerotermes* species. *M. crassus* proved to be somewhat more resistant to desiccation than *M. championi*. The difference in the average longevity of both *Microcerotermes* species was greater at lower than at higher atmospheric moisture. At lower percentages of relative humidity *M. crassus* proved to be a little more resistant to drying than *R. tibialis* and *R. hesperus*, but at higher atmospheric moisture the longevity of *R. hesperus* and *M. crassus* was about the same.

Prorhinotermes simplex and *Nasutitermes nigriceps* showed about the same resistance to desiccation at all stages of atmospheric moisture. *Coptotermes formosanus* was slightly more susceptible than *N. nigriceps* and *P. simplex* at lower atmospheric moisture but at higher relative humidity these three species showed about the same resistance to desiccation.

At 33 to 93 % relative humidity *R. lucifugus* (from Francavilla) survived slightly longer than *R. santonensis*, but at higher

Table 21

Comparison between average survival of workers or pseudergates of the following species of termites under starvation conditions in relation to different stages of relative humidity

Species of termites	Average survival in days in relation to relative humidity						
	33 %	63 %	75 %	85 %	93 %	98 %	100 %
Kalotermitidae							
<i>C. dudleyi</i>	58.8	59.0	60.2	59.9	56.5	45.0	30.5
<i>K. flavicollis</i>	49.2	56.9	62.3	63.5	63.9	57.2	28.2
<i>N. jouteli</i>	15.9	20.5	26.1	28.5	29.9	31.5	25.5
Termopsidae							
<i>Z. angusticollis</i>	14.7	17.8	26.7	41.2	49.5	52.2	55.5
Rhinotermitidae							
<i>H. indicola</i> (from 30°C culture)	3.9	6.5	10.7	13.5	20.3	27.8	33.4
<i>H. indicola</i> (from 26°C culture)	3.5	5.9	9.5	12.7	17.9	23.6	30.5
<i>R. tibialis</i>	3.1	3.9	4.5	6.9	8.4	16.2	24.0
<i>R. hesperus</i>	2.4	3.8	5.3	6.7	13.2	19.1	21.1
Termitidae							
<i>M. crassus</i>	4.0	6.8	8.2	10.4	15.9	19.1	20.3
<i>M. championi</i>	2.5	3.9	5.9	7.1	10.0	15.6	18.9
<i>N. nigriceps</i>	2.9	3.9	5.0	6.0	10.1	13.2	15.2
Rhinotermitidae							
<i>P. simplex</i>	2.7	4.3	6.0	8.2	10.2	14.4	15.9
<i>C. formosanus</i>	2.1	2.9	3.8	5.3	8.1	11.2	15.4
<i>R. santonensis</i>	1.9	3.1	4.6	5.7	9.3	11.6	12.6
<i>R. lucifugus</i> (from Favone)	1.7	2.4	3.4	4.7	9.8	16.5	18.4

Species of termites	Average survival in days in relation to rela- tive humidity						
	33 %	63 %	75 %	85 %	93 %	98 %	100 %
<i>R. lucifugus</i> (from Franca- villa)	2.6	4.3	5.1	7.4	11.2	11.6	12.0
<i>R. lucifugus</i> (from Munich)	1.6	2.1	2.9	3.7	5.8	6.6	6.8
<i>R. speratus</i> <i>kyushuensis</i>	1.0	1.8	2.5	4.0	7.7	11.3	12.0
<i>R. flavipes</i> (from Hallein)	1.7	2.6	3.4	4.4	7.1	10.7	11.5
<i>R. flavipes</i> (from Hamburg)	2.2	3.2	4.4	5.2	7.3	9.3	9.9
<i>R. flavipes</i> (from Charles- ton)	1.2	1.6	2.0	2.8	3.8	6.7	9.1
<i>R. virginicus</i>	1.8	2.4	3.4	4.9	7.2	8.9	11.1
<i>R. speratus</i> <i>speratus</i>	1.2	1.9	2.4	3.3	4.1	5.0	7.6
<i>C. niger</i>	1.2	1.7	2.1	2.8	4.8	5.9	7.7

Table 22

Comparison between the average survival of workers and soldiers of *Heterotermes indicola*, *Coptotermes formosanus*, *Microcerotermes crassus*, *Microcerotermes championi*, *Nasutitermes nigriceps*, *Reticulitermes flavipes* from Charleston and *Coptotermes niger* under starvation conditions in relation to relative humidity

Species of termites	caste and group size	Average survival in days at different stages of relative humidity							
		33 %	63 %	75 %	85 %	93 %	98 %	100 %	
H. indicola (from 30°C culture)	30 W ^{a)} 5 S ^{b)}	3.9 1.9	6.5 2.4	10.7 3.4	13.5 3.9	20.3 6.6	27.8 8.2	33.4 8.9	
C. formosanus	20 W 20 S	2.1 1.7	2.9 2.0	3.8 2.6	5.3 2.9	8.1 4.2	11.2 4.6	15.4 5.4	
M crassus	10 W 10 S	4.0 2.3	6.8 3.5	8.2 4.6	10.4 6.6	15.9 9.7	19.1 9.8	20.3 8.2	
M. championi	20 W 5 S	2.5 1.4	3.9 2.2	5.9 3.1	7.1 4.1	10.0 5.8	15.6 8.4	18.9 10.8	
N. nigriceps	20 W 20 S	2.9 2.6	3.9 3.8	5.0 4.7	6.0 5.6	10.1 8.2	13.2 8.2	15.2 8.8	
R. flavipes (from Charleston)	20 W 5 S	1.2 1.3	1.6 1.9	2.0 2.1	2.8 2.9	3.8 4.0	6.7 4.8	9.1 7.3	
C. niger	20 W 20 S	1.2 1.5	1.7 2.0	2.1 2.2	2.8 2.9	4.8 3.9	5.9 4.6	7.7 5.2	

a) workers

b) soldiers

atmospheric moisture both species showed about the same resistance to drying. *R. lucifugus* from three different geographical origins (from Francavilla, Favone and Munich ¹⁾) showed a different resistance to desiccation mainly at higher stages of relative humidity.

R. speratus kyushuensis, *R. flavipes* and *R. virginicus* revealed about the same resistance to desiccation but they were slightly more susceptible than *R. lucifugus* (except *R. lucifugus* from Munich) and *R. santonensis*.

These investigations showed that *R. speratus speratus* and *C. niger* were most susceptible ones of all species of termites kept under starvation conditions at different percentages of relative humidity.

3.1.2.2. Comparison between the average survival of workers and soldiers

The difference between the desiccation resistance of workers and soldiers (Table 22) varied from species to species. The difference in the average survival of workers and soldiers of all the species of termites increased with the increasing of atmospheric moisture. Therefore, the difference in the susceptibility of workers and soldiers was lowest at 33 % and highest at 100 % relative humidity.

In the case of *H. indicola*, *C. formosanus*, *M. championi*, *M. crassus* and *N. nigriceps*, workers survived longer than soldiers at all stages of relative humidity. At lower atmospheric moisture (33 to 75 %) soldiers of *C. niger* survived somewhat longer than workers. Above 85 % relative humidity workers showed a slightly greater resistance against drying than soldiers.

1) The cultured insects were collected in Munich. But, most probably the geographical origin of this termite is North Italy.

Between 33 and 93 % relative humidity soldiers of *R. flavipes* from Charleston survived slightly longer than workers, whereas, at 98 and 100 % relative humidity workers proved to be more resistant to desiccation than soldiers.

H. indicola and *C. formosanus* showed the greatest difference in the survival period of workers and soldiers, *M. championi*, *M. crassus* and *N. nigriceps* intermediate and *C. niger* and *R. flavipes* showed the smallest difference in the survival period of workers and soldiers.

The body weight of the workers of *N. nigriceps* was about 2 to 2 1/2 times greater than the body weight of soldiers. But in the case of other species, workers and soldiers of a species showed about the same body weight. These studies also proved that the differences in the rate of survival period of workers and soldiers were independent from the body weight of the workers and soldiers.

3.1.2.3. Comparison between the average survival of workers and soldiers in heterogenous groups (workers and soldiers together in each test group)

Tests with heterogenous groups showed (Table 23) that the soldiers of *N. nigriceps*, *C. niger* and *R. flavipes* were somewhat more resistant than workers at all the stages of atmospheric moisture. In the case of *C. formosanus* workers proved to be more resistant than soldiers.

The average survival of soldiers in heterogenous groups (Table 23) was higher than the average survival of soldiers in homogenous groups (Table 22). On the other hand, the survival period of workers in heterogenous groups (Table 23) was shorter compared with the survival period of workers in homogenous groups (Table 22). This increase in the survival period of soldiers and the decrease in the survival period of workers in heterogenous groups was due to trophalaxis among the worker caste. Workers fed each other when they were tested in homogenous groups. But in heterogenous groups soldiers were also

Table 23

Average survival of workers and soldiers in heterogenous groups of *Reticulitermes flavipes* (from Charleston), *Coptotermes formosanus*, *Coptotermes niger* and *Nasutitermes nigriceps* under starvation conditions at different percentages of relative humidity

Species of termites	Group composition	Average survival of workers and soldiers in relation to relative humidity							
		33 %	63 %	75 %	85 %	93 %	98 %	100 %	
<i>R. flavipes</i> (from Charleston)	20 W + W ^{a)}	1.2	1.7	2.2	3.1	4.1	6.1	6.8	
	5 S S ^{b)}	1.5	1.9	2.4	3.6	4.7	6.5	8.9	
<i>C. niger</i>	20 W + W	1.0	1.2	1.5	2.2	4.1	5.7	5.9	
	10 S S	1.4	2.1	2.7	2.5	4.8	5.9	6.1	
<i>N. nigriceps</i>	20 W + W	2.9	3.5	4.7	5.9	9.8	12.1	12.7	
	10 S S	3.2	4.4	5.9	8.1	11.1	12.5	12.8	
<i>C. formosanus</i>	20 W + W	2.1	2.9	3.6	5.1	7.4	8.2	11.0	
	10 S S	1.8	2.6	3.2	4.1	5.2	5.2	6.4	

a) workers

b) soldiers

fed by workers. This caused an increase in the survival period of soldiers and a decrease in the survival period of workers.

3.1.2.4. Comparison between the average survival of isolated and grouped workers

Investigations with isolated and grouped workers showed (Table 24) that isolated workers were more susceptible to desiccation than grouped workers of all species of termites at various stages of relative humidity. The difference in desiccation resistance of single and grouped workers increased with the raising of atmospheric moisture. Near 100 % relative humidity the isolated and grouped workers showed the highest difference in the survival period.

Desiccation resistance of isolated and grouped workers varied from species to species. *N. nigriceps*, *M. crassus* revealed the highest difference in the susceptibility of isolated and grouped workers, *C. formosanus* intermediate and *Reticulitermes* species showed the smallest difference in the survival period of isolated and grouped workers. Four *Reticulitermes* species showed about the same difference in the average survival of grouped and isolated workers (Table 24).

3.1.2.5. Comparison between the average survival of isolated and grouped soldiers

Isolated soldiers proved more susceptible to desiccation compared with grouped soldiers (Table 25). The difference in the survival period of grouped and isolated soldiers increased with the raising the atmospheric moisture. At the highest (100 %) relative humidity grouped and isolated soldiers showed a maximum difference in the average survival. Like the workers, the difference in the susceptibility of isolated and grouped soldiers also varied from species to species. *C. formosanus*,

Table 24

Comparison between differences in the average survival of isolated and grouped workers of *Nasutitermes nigriceps*, *Microcerotermes crassus*, *Coptotermes formosanus*, *Reticulitermes flavipes* from Hamburg, *R. lucifugus* from Francavilla, *R. santonensis* and *R. virginicus* under starvation conditions in relation to relative humidity

Species of termites	Group size	Average survival of isolated and grouped workers in relation to relative humidity							
		33 %	63 %	75 %	85 %	93 %	98 %	100 %	
<i>N. nigriceps</i>	20 W ^{a)}	2.9	3.9	5.0	6.0	10.1	13.2	15.2	
	1 W	1.8	2.6	3.2	2.8	4.9	6.1	6.2	
<i>M. crassus</i>	10 W	4.0	6.8	8.2	10.4	15.9	19.1	20.3	
	1 W	2.8	3.9	5.2	7.2	8.2	10.9	12.6	
<i>C. formosanus</i>	20 W	2.1	2.9	3.8	5.3	8.1	11.1	15.4	
	1 W	1.4	2.5	2.7	3.7	5.1	7.5	10.5	
<i>R. flavipes</i> Hamburg	10 W	2.2	3.2	4.4	5.2	7.3	9.3	9.9	
	1 W	2.0	2.6	3.6	4.8	6.5	8.2	8.6	
<i>R. lucifugus</i> Francavilla	10 W	2.6	4.3	5.1	7.4	11.2	11.6	12.0	
	1 W	1.4	2.2	3.0	5.4	7.4	9.6	9.8	
<i>R. santonensis</i>	10 W	1.9	3.1	4.6	5.7	9.3	11.6	12.6	
		1.8	2.4	3.2	4.8	7.6	9.4	11.4	
<i>R. virginicus</i>	10 W	1.8	2.4	3.4	4.9	7.2	8.9	11.1	
	1 W	1.6	2.0	3.2	4.4	5.5	8.6	9.2	

a) workers

M. crassus and *N. nigriceps* showed successively increasing differences in the average survival of isolated and grouped soldiers.

Due to trophallaxis, among the worker the difference between the longevity of isolated and grouped workers (Table 24) was greater than the difference between the longevity of isolated and grouped soldiers (Table 25).

Table 25

Comparison between the average survival of isolated and grouped soldiers of *Nasutitermes nigriceps*, *Microcerotermes crassus*, *Coptotermes formosanus* under starvation conditions in relation to relative humidity

Species of termites	Group size	Average survival of isolated and grouped soldiers in relation to relative humidity							
		33 %	63 %	75 %	85 %	93 %	98 %	100 %	
<i>N. nigriceps</i>	20 S ^{a)}	2.6	3.8	4.7	5.6	8.2	8.2	8.8	
	1 S	1.8	2.0	3.0	3.4	4.6	4.9	5.0	
<i>M. crassus</i>	10 S	2.3	3.5	4.6	6.6	9.7	9.8	8.2	
	1 S	1.4	2.2	3.7	5.5	7.7	7.3	7.6	
<i>C. formosanus</i>	20 S	1.7	2.0	2.6	2.9	4.2	4.6	5.4	
	1 S	1.0	1.5	1.8	2.1	2.3	2.6	3.4	

a) soldiers

3.2. Effect of humidity upon the feeding and develop-
ment of termites

3.2.1. Results with different species

3.2.1.1. *Kaloterms flavicollis* (Fabricius)

Test period 1 - 4 weeks

As shown in Fig. 26 the wood consumption and mortality of insects was about similar at all stages of water content of vermiculite (50 to 400 % water). At all stages of water content the mortality of animals was about 5 to 13 % and the body weights of living insects were not changed.

No new caste (soldiers, neotenics, imagines) was developed within the first four weeks of the test.

Test period 5 - 8 weeks

During this period again, the wood consumption and mortality (2 - 14 %) was similar at all the stages of water content of the substrate. There was very little increase in the body weights of living insects. The imagines developed in all the groups but pre-soldiers and neotenics only in some groups.

The imagines (some of which were eaten by the pseudergates) and dead pseudergates were replaced by new pseudergates up to the original group size of 50 individuals and the weight of the groups was determined again.

Test period 9 - 16 weeks

During 9 - 16 weeks also, the feeding quantity and survival of insects was not effected by the water content of substrate. The number of surviving insects was 87 to 92 %. The body weight of surviving insects was a little increased. At all the stages of water content, the increase in the bodyweight of insects was about the same.

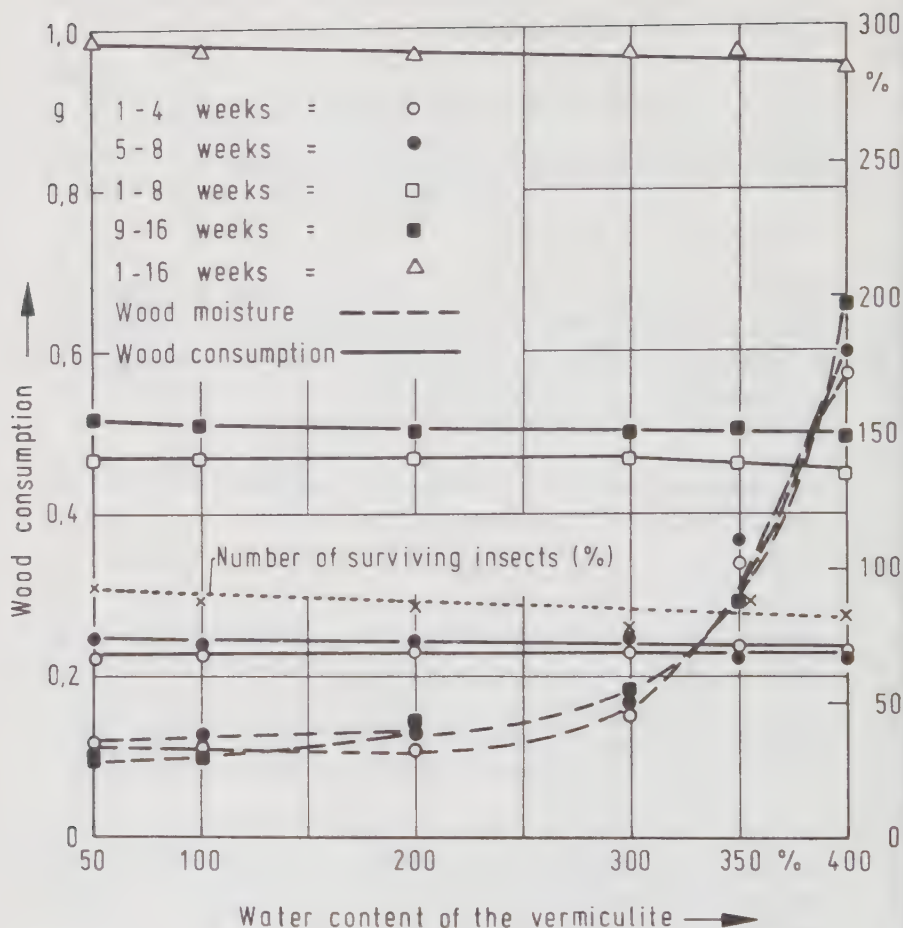


Fig. 26 - Wood consumption, wood moisture (pine sapwood) and percentage of living insects (after 16 weeks) of *Kaloterмес flavicollis* in relation to water content of the vermiculite at 26°C and 98 to 99 % relative humidity of the room after different test period (average from 3 replications).

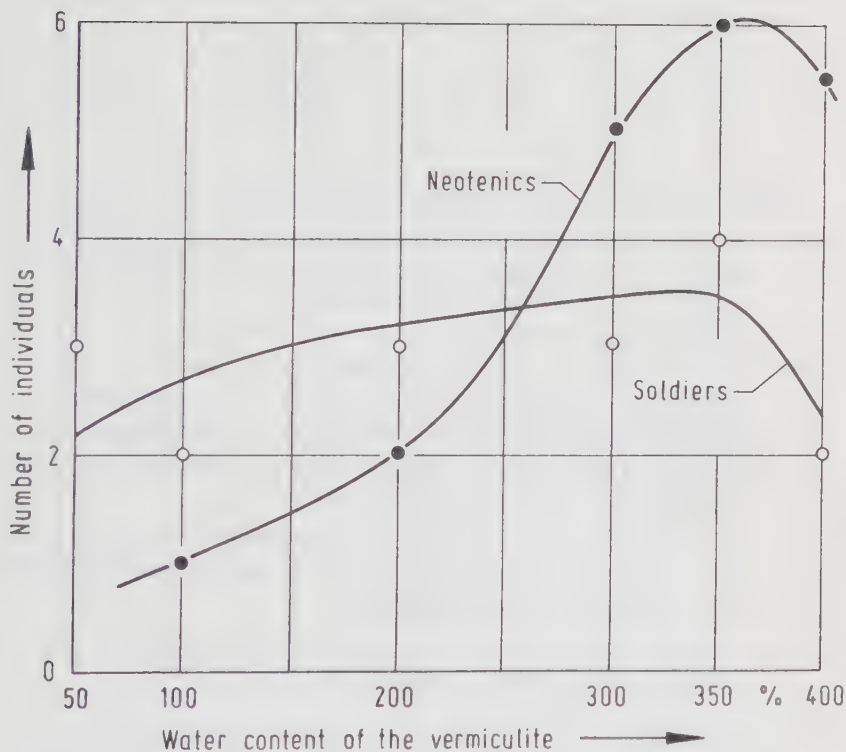


Fig. 27 - Newly developed neotenics and soldiers of *Kaloterмес flavicollis* in relation to the water content of the vermiculite at 26°C and 98 to 99 % relative humidity after 16 weeks (total of 3 replications).

All the groups were still living after 16 weeks.

The number of newly developed imagines was similar at all the stages of water content. Between 50 and 350 % water content the number of newly developed soldiers increased slowly but above 350 % moisture content the number of newly developed soldiers decreased rapidly. The number of newly developed neotenics was increased, slowly from 50 to 200 % water content, strongly from 200 to 350 % water and was decreased above 350 % water content of the vermiculite (Fig. 27).

The wood deterioration and the mortality of insects was about the same during the first and second four weeks. The wood deterioration and the percentage of surviving insects was larger within 9 - 16 weeks compared to 1 - 8 weeks (1 - 4 + 5 - 8 weeks). Increased wood deterioration in the last 8 weeks (9 - 16 weeks) may be due to the raising of weight of insects, no disturbance and adaptation of insects to experimental conditions. The total amount of the wood consumption in 16 weeks was also similar at all the stages of water content of vermiculite.

These studies showed that wood consumption and survival of *K. flavicollis* was independent from water content (between 50 and 400 %) of the vermiculite.

3.2.1.2. *Zootermopsis angusticollis* (Hagen)

Test period 1 - 4 weeks

At 100 to 300 % water content of vermiculite the wood consumption was about the same and from 300 to 400 % water content there was a slow reduction in the wood consumption (Fig. 28). The ratio between the maximum (100 to 300 % water) and minimum (400 % water) amount of wood consumption was about 1.8 : 1. The mortality was 15 % at 100 % moisture content and from 200 to 400 % moisture content the mortality was reduced to about 7 to 10 %. There was a minute decrease in the body weight of insects and no individual of a new caste was developed at all the stages of moisture content of the substrate.

Test period 5 - 8 weeks

During this period the wood consumption was about similar at all the stages of moisture content of vermiculite. Mortality of insects was 3 % at lowest stage of water content and 10 to 15 % at 200 to 400 % water content and the weight of surviving individuals was a little improved. Neotenics were developed, in some groups at 200 to 400 % water content of vermiculite.

At the end of 8 weeks the dead pseudergates were replaced by new ones up to the original group size of 15 individuals and the weight of each group was determined.

Test period 9 - 16 weeks

The wood consumption was raised slowly from 100 to 200 % water content and reduced slowly at 200 to 300 % water content of the substrate. But from 300 to 400 % water content the insects consumed about the same amount of wood. The minimum amount of wood consumption at 300 to 400 % water content was about 93 % of the maximum amount of wood consumption at 200 % water content of vermiculite.

The mortality was increased from 9 to 15 % with the increasing of the water content of vermiculite (100 to 400 % water). Body weight of insects was a little increased. No soldier or imago developed within 16 weeks. The number of newly developed neotenics increased with the raising of moisture content of the substrate (Fig. 29).

The wood deterioration increased in the second four weeks compared with the first four weeks of the test. Similarly, the wood deterioration was more during the last 8 weeks (9 - 16 weeks) in comparison with the first 8 weeks (1 - 4 + 5 - 8 weeks). This difference may be due to no disturbance, increase in body weight and adaptation of the insects to experimental conditions.

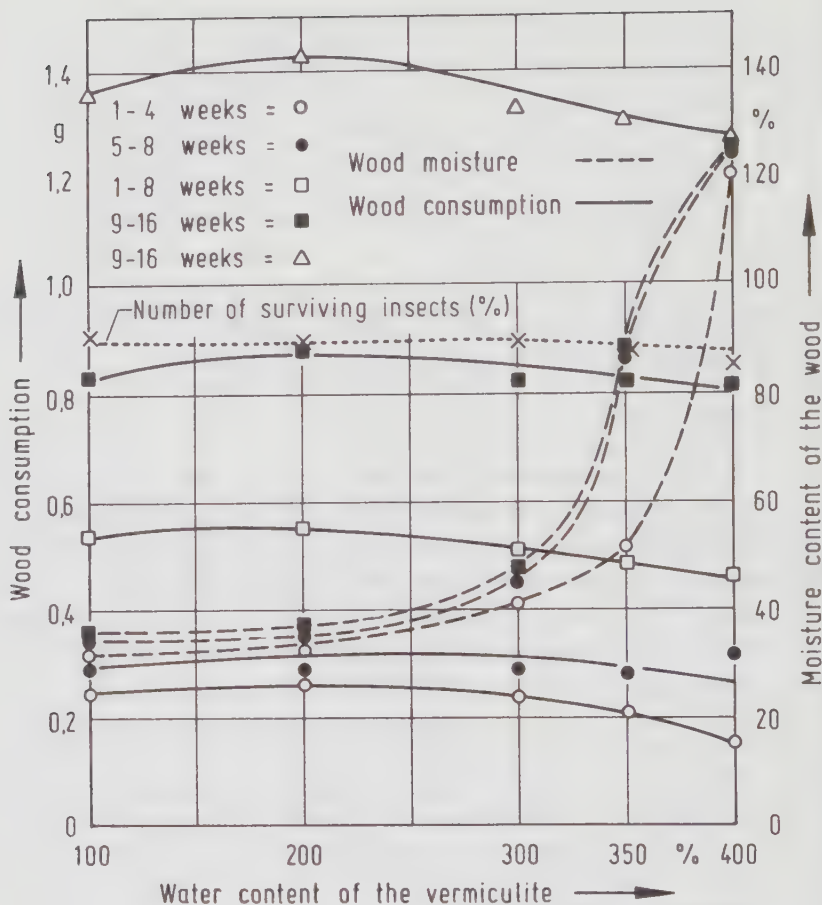


Fig. 28 - Wood consumption, wood moisture (pine sapwood) and percentage of surviving insects (after 16 weeks) of *Zootermopsis angusticollis* in relation to the water content of the vermiculite at 20°C and 98 to 99 % relative humidity of the room after different test periods (average of 3 replications).

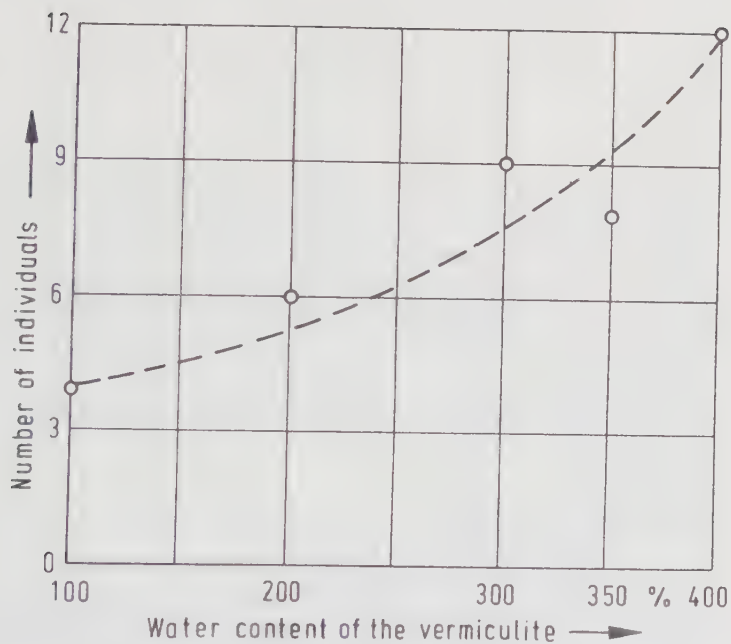


Fig. 29 - Newly developed neotenics of *Zootermopsis angusticollis* in relation to water content of the vermiculite at 20°C and 98 to 99 % relative humidity of the room after 16 weeks (total of 3 replications).

Total feeding quantity was highest at 200 % and lowest at 400 % water content of the substrate after 16 weeks. These investigations proved that 150 to 250 % water content of the vermiculite was the optimum for testing and culturing of *Z. angusticollis*.

3.2.1.3. *Heterotermes indicola* (Wasmann)

Test period 1 - 4 weeks

The wood consumption (Fig. 30) was raised slowly between 100 and 200 % water content of vermiculite. Between 200 and 300 % water content the amount of wood consumption was about the same and was reduced slowly from 300 to 400 % water content of vermiculite. The lowest amount of feeding quantity - at 400 % water content - was about 79 % of the optimum amount of wood consumption at 200 to 300 % water content. At 100 and 350 % moisture content the insects deteriorated about the same quantity of wood.

Test period 5 - 8 weeks

From 100 to 200 % water content the amount of the wood consumption increased and between 200 and 400 % water content the feeding quantity was about similar. The minimum amount of wood consumption - at 100 % water content - was about 75 % of the maximum amount of wood consumption at 200 to 400 % water content of the vermiculite.

At 100 % water content the wood degradation was more during

Fig. 30 - Wood consumption, wood moisture (pine sapwood) and percentage of surviving insects (after 16 weeks) of *Heterotermes indicola* in relation to water content of the vermiculite at 26°C and 90 % relative humidity of the room after different test periods (average of 3 replications).

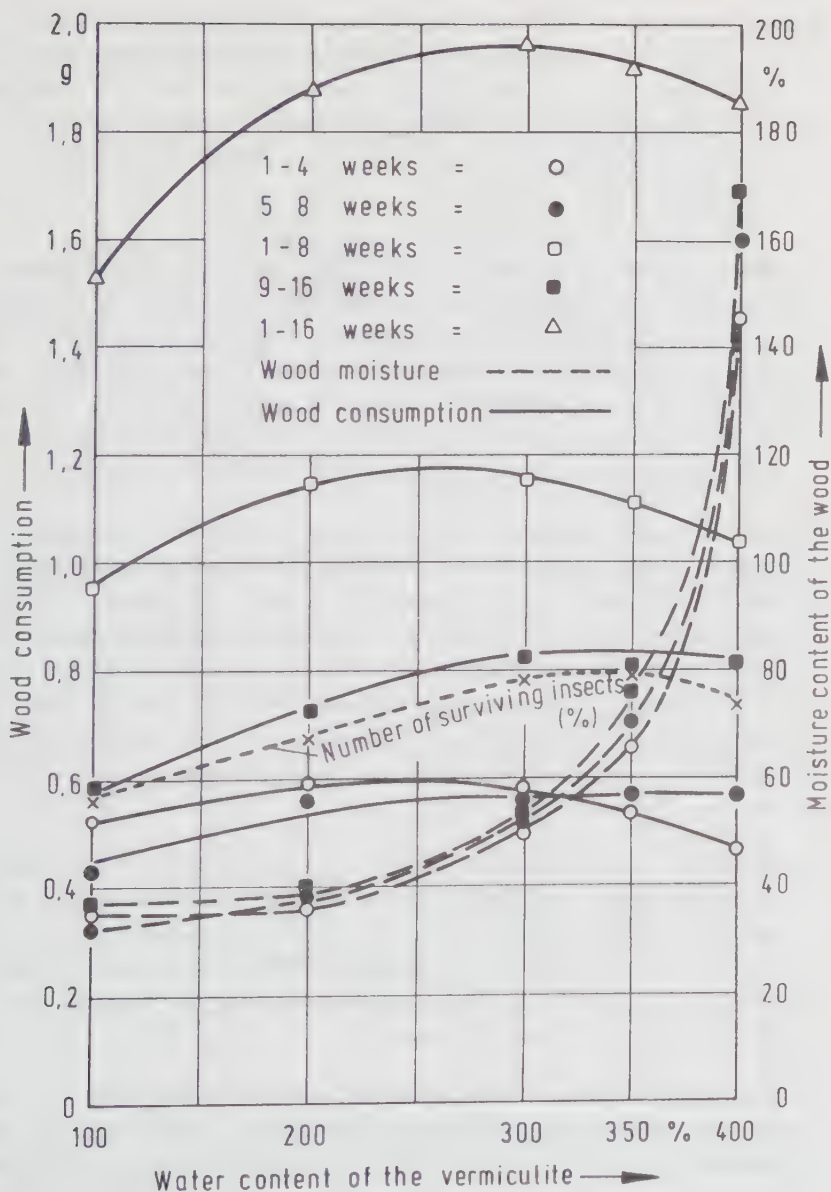


Fig. 30

the first four weeks in comparison with the second four weeks, but from 200 to 350 % water content, the wood degradation was about the same. At 400 % water content the insects deteriorated a greater amount of wood during the second four weeks (5 - 8 weeks) compared with the first four weeks (1 - 4 weeks).

Test period 9 - 16 weeks

After 9 - 16 weeks there was a slow increase in the amount of wood consumption with the raising of water content of the vermiculite from 100 to 300 %. Between 300 and 400 % water content the insects consumed about the same amount of wood. The minimum wood consumption - at 100 % water content - was about 70 % of the optimum amount of wood consumption at 300 to 400 % water content of the substrate.

In the first 8 weeks (1 - 4 + 5 - 8 weeks) the wood deterioration was the highest at 200 to 300 % moisture content but in the last 8 weeks (9 - 16 weeks) the maximum amount of wood was deteriorated at 300 to 400 % water content of the vermiculite. The wood consumption was higher during the first 8 weeks (1 - 8 weeks) than the last 8 weeks (9 - 16 weeks). With increased water content of vermiculite, the difference in the quantity of wood consumption was slowly reduced between 1 - 8 and 9 - 16 weeks.

The total feeding quantity after 16 weeks showed that the insects consumed a minimum amount of wood at 100 % and a maximum amount at 300 % water content of the vermiculite. At 350 % water content the insects consumed a little less than at 300 %. The insects consumed about the same amount of wood at 200 and at 400 % water after 16 weeks.

Increased amount of wood consumption at higher stages of water content during the test proved the better adaptation of the insects to a higher percentage of water content of substrate.

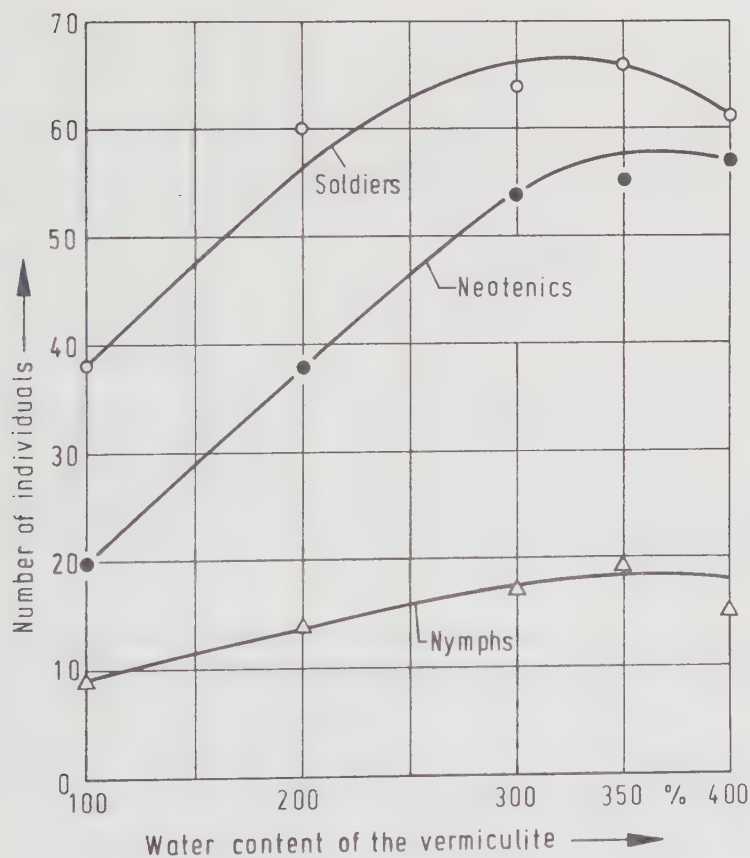


Fig. 31 - Development of nymphs, soldiers and neotenics with *Heterotermes indicola* in relation to water content of the vermiculite at 26°C after 16 weeks (total of 3 replications).

H. indicola build galleries at all the stages of water content of the vermiculite. But at 300 to 400 % water content the gallery building was larger.

The minimum number of surviving insects (after 16 weeks) was 57.5 % at 100 % water content, which increased up to 68 % at 200 % water content and 79 to 79.5 % at 300 to 350 % water content of the vermiculite. But from 350 to 400 % moisture content of the substrate the number of surviving insects was reduced to 73.5 %. The surviving insects showed a minute decrease in bodyweight.

The total number of newly developed soldiers, neotenics and nymphs (from 3 replications after 16 weeks) in relation to the water content of the vermiculite at 26°C is shown in Fig. 31. With increase of the water content of vermiculite from 100 to 300 % the number of new developed soldiers was raised very rapidly (38 at 100 % and 60 at 200 % water content). The raising of the water content of vermiculite from 350 to 400 % had a slowly reducing effect on the development of soldiers.

The development of new neotenics was increased rapidly from 20 (at 100 % water) to 38 (at 200 % water) up to 54 at 300 % water content of the vermiculite. But between 300 and 400 % water content the development of neotenics was not increased. The number of neotenics at 100 % water content was about 30 % of the maximum number at 400 % water content of the substrate.

The development of nymphs was increased slowly with the increase of the water content of the vermiculite. The minimum and maximum number of nymphs was 9 and 19 at 100 and 350 % water content of the substrate respectively (Ratio 1 : 2).

These studies have shown that 300 to 350 % water content of the vermiculite was the optimum for testing and culturing of *H. indicola* (G. Becker and M. Lenz, 1970).

3.2.1.4. *Coptotermes formosanus* (Shiraki)

Test period 1 - 4 weeks

As shown in Fig. 32 the insects consumed the smallest amount of wood at 100 % water content of vermiculite. With increasing of water content of the substrate from 100 to 350 %, the quantity of wood consumption also increased. But between 350 and 400 % water content of the substrate there was only a slight increase in the amount of wood consumption. The ratio between the minimum (100 % water content) and maximum quantity of wood consumption (350 to 400 % water content) was 1 : 2.3.

Test period 5 - 8 weeks

During this time the insects consumed minimum amount of wood at 100 % water content again. From 100 to 200 % water content there was a little increase in the amount of wood consumption, which then was increased about twice from 200 to 300 % water content. Between 300 and 400 % water content of substrate the insects did not show any change in their feeding activities.

The ratio between minimum (at 100 % water content) and maximum amount of wood consumption (at 300 to 400 % water content) was 1 : 3.5 after 5 - 8 weeks.

At 100 to 200 % water contents of the vermiculite the insects consumed more wood in the first four weeks than in the second four weeks. However, the wood consumption was about the same at 300 to 400 % water content of the vermiculite during the first and the second four weeks.

Fig. 32 - Wood consumption, wood moisture (pine sapwood) and percentage of surviving insects (after 16 weeks) of *Coptotermes formosanus* in relation to the water content of the vermiculite at 26°C and 90 % relative humidity of the room after different test periods (average of 3 replications).

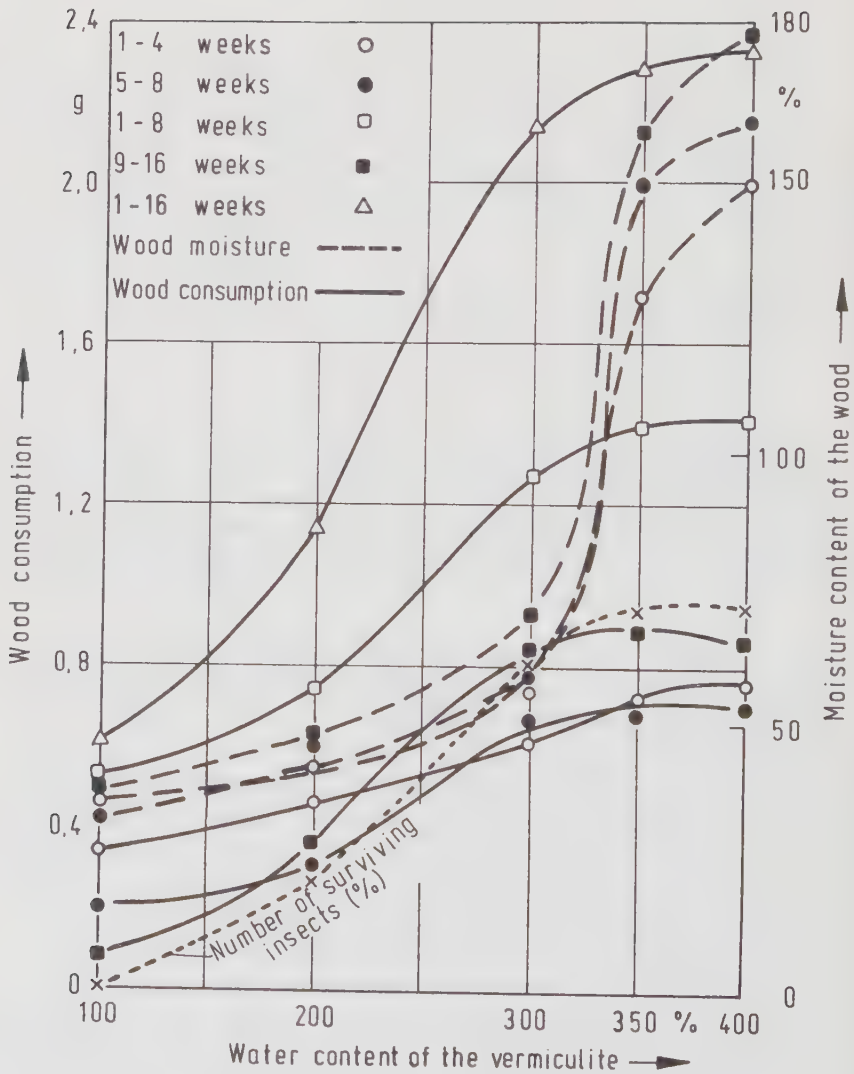


Fig. 32

Test period 9 - 16 weeks

Between 9 and 16 weeks the wood consumption at 100 % water content of vermiculite was very small. With the increase of percentage of water content of the substrate from 100 to 300 % , the feeding activities of insects raised strongly. Between 300 and 400 % water content the wood consumption was about the same. The ratio between the minimum (at 100 % water content) and maximum amount of wood consumption (at 300 % to 400 % water content) was about 1 : 9.

In 1 - 8 weeks (1 - 4 + 5 - 8 weeks) the insects consumed more wood than in 9 - 16 weeks. The maximum amount of wood consumption after 1 - 8 and 1 - 16 weeks was at 350 to 400 % water content of vermiculite. The reduced amount of wood consumption during the last 8 weeks (9 - 16) in comparison with the first 8 weeks (1 - 8) was due to the mortality of animals.

At 100 % water content of vermiculite the first group was dead after 5 weeks, the second after 8 weeks and the thirs or last group after 10 weeks. At 200 % water content of the substrate one group was dead after 8 weeks. But in the rest of the groups the different number of insects was surviving up to 16 weeks. The highest number of surviving insects after 16 weeks was about 70 % at 350 to 400 % water content of substrate. These investigations showed that 350 to 400 % water content of vermiculite is optimum for testing and culturing of *C. formosanus*.

3.2.1.5. *Reticulitermes flavipes* (Kollar) from Hamburg

Test period 1 - 4 weeks

In the first four weeks the minimum amount of the wood consumption was at 100 % water content of the substrate (Fig. 33). From 100 to 300 % water content, the wood consumption increased

strongly. At 350 % water content the quantity of wood consumption was the maximum and at 300 and 400 % water content the insects consumed about the same amount of wood. The ratio between maximum (at 350 % water content) and minimum (at 100 % water content) quantity of wood consumption was 3.3 : 1. At 100 % water content of the substrate the first group was dead after 3 weeks, the second and the third or last group after 4 weeks.

Test period 5 - 8 weeks

There was a gradual increase in the amount of wood consumption with raising water content of vermiculite and the maximum amount of wood consumption was at 400 %. The ratio between the quantity of wood consumption at 400 and 200 % water content was 3.4 : 1 after the second four weeks.

At 200 % water content the first group was dead after 5 weeks, the second after 6 weeks and the third or last group after 7 1/2 weeks.

From 100 to 350 % water content the amount of the wood consumption was higher in the first four weeks than in the second four weeks. But at 400 % water content the insects consumed about the same amount of wood during the first and the second four weeks.

Test period 9 - 16 weeks

In 9 - 16 weeks the insects consumed somewhat less wood at 300 % than at 350 to 400 water content. At 350 % moisture content the amount of wood consumption was slightly more than at 400 % moisture content of the substrate.

Fig. 33 - Wood consumption, wood moisture (pine sapwood) and percentage of surviving insects (after 16 weeks) of *Reticulitermes flavipes* from Hamburg in relation to water content of the vermiculite at 26°C and 90 % relative humidity of the room after different test periods (average from 3 replications).

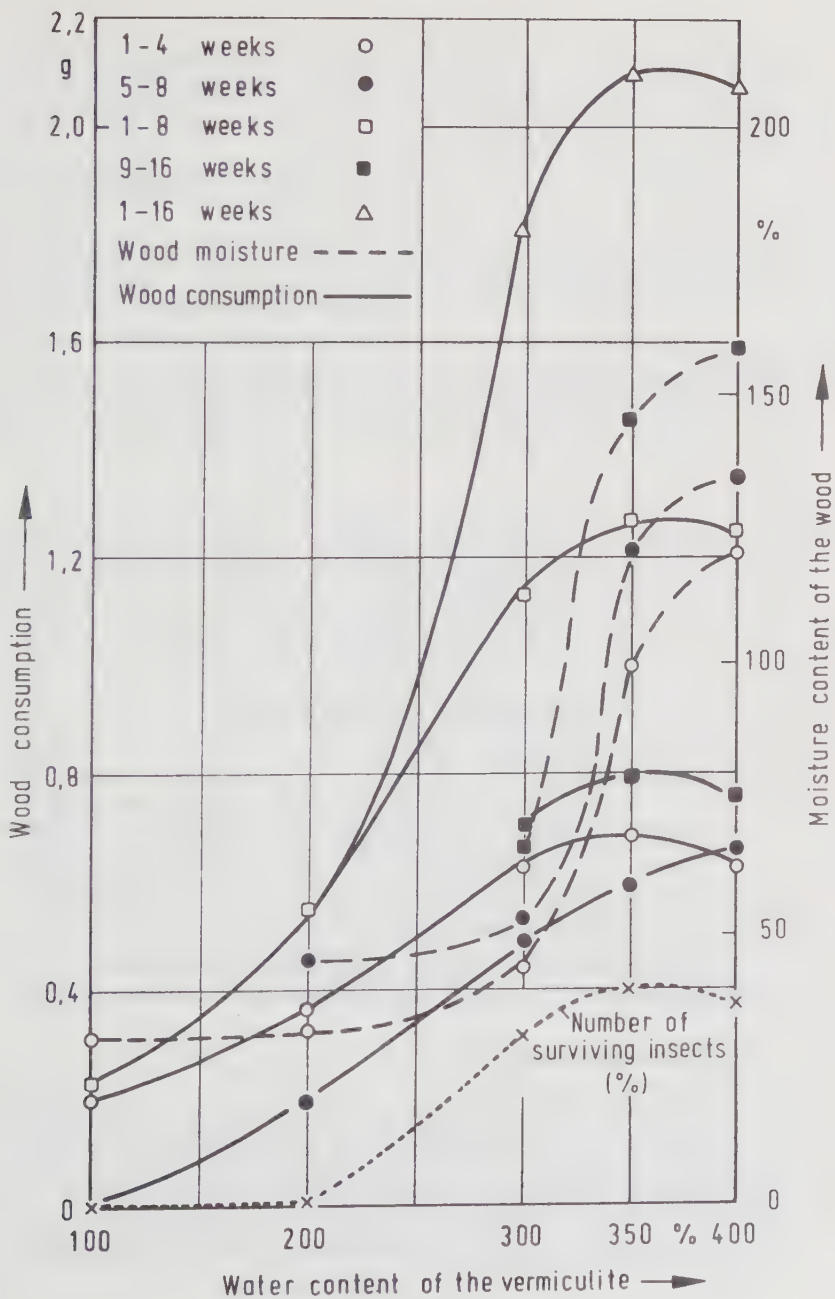


Fig. 33

In 1 - 8 weeks (1 - 4 + 5 - 8 weeks) the quantity of wood consumption was larger than in 9 - 16 weeks due to the high mortality in the last 8 weeks.

Total amount of wood consumption after 1 - 8 and 1 - 16 weeks was maximum at 350 to 400 % water content of vermiculite.

The number of surviving insects was 37 % at 300 %, 47 % at 350 % and 45 % at 400 % water content of vermiculite.

The total number of newly developed nymphs (from 3 replications) was 46 at 300 %, 61 at 350 % and 66 at 400 % water content of the vermiculite. Between 300 and 400 % water content the number of newly developed soldiers was about the same (6 - 7).

These studies showed that humidity of the substrate has a great effect on *R. flavipes*. 350 to 400 % water content of vermiculite is the most suitable for testing and culturing of this species (G. Becker and M. Lenz, 1970).

3.2.1.6. *Microcerotermes championi* Snyder

Test period 1 - 4 weeks

The maximum amount of wood consumption (Fig. 34) during the first four weeks was between 100 and 300 % water content. Above 300 % moisture the quantity of wood consumption was reduced gradually to the minimum at 400 %. Wood consumption at 400 % water content was about 75 % of the maximum wood consumption at 100 to 300 % water content of the substrate.

Test period 5 - 8 weeks

During 5 - 8 weeks the insects consumed a maximum amount of wood at 100 to 200 % water content. From 200 to 400 % water content the feeding quantity descended slowly to the minimum at 400 % water content of the vermiculite again. The minimum wood consumption at 400 % was about 70 % of the optimum wood consumption at 100 - 200 % water content.

In 1 - 4 weeks the quantity of wood consumption was about twice the size in comparison with the quantity of wood consumption in 5 - 8 weeks.

Test period 9 - 16 weeks

From 100 to 200 % water content the quantity of the wood consumption was raised slowly. At 200 to 350 % water content the insects consumed the maximum amount of wood. From 350 to 400 % water content the feeding quantity was reduced gently to the minimum at 400 % water content. Ratio between the minimum (at 400 % water) and maximum (at 200 to 350 % water) of wood consumption was about 1 : 1.8 after 9 - 16 weeks.

In 1 - 8 weeks the insects destroyed more wood at 100 % water content than at 350 % water content. But in 9 - 16 weeks the wood destruction was more at 350 % water content than at 100 % water content. This was due to a higher mortality at low moisture content of vermiculite.

In the first four weeks (1 - 4 weeks) the insects deteriorated a higher quantity of wood than during the last 8 weeks (9 - 16 weeks). In 1 - 8 weeks (1 - 4 + 5 - 8 weeks) the wood deterioration was about twice than in 9 - 16 weeks. The reduction in wood deterioration was due to mortality of animals during the experiment.

The curve of the total amount of wood consumption after 1 - 16 weeks was raised slowly at 100 to 200 % water content. From 200 to 300 % water content the wood consumption was reduced

Fig. 34 - Wood consumption, wood moisture (birch wood) and percentage of surviving insects (after 16 weeks) of *Microcero-termes championi* in relation to water content of the vermiculite at 28°C and 95 to 98 % relative humidity of the room after different test periods (average of 3 replications).

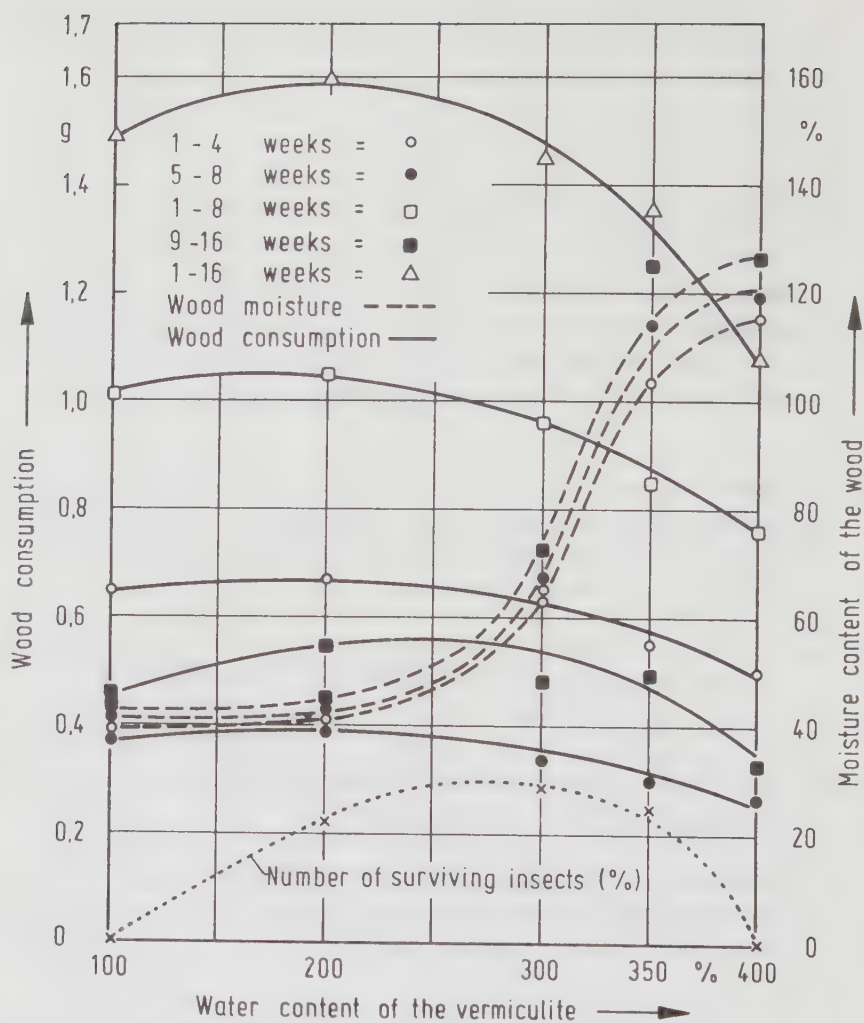


Fig.34

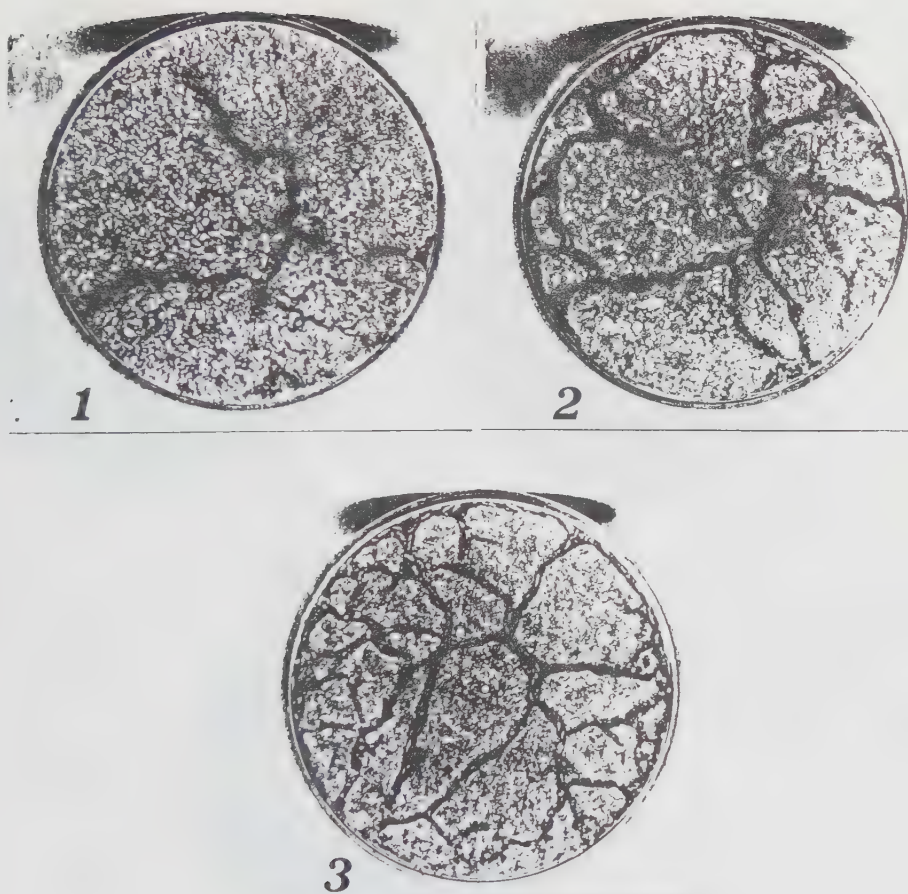
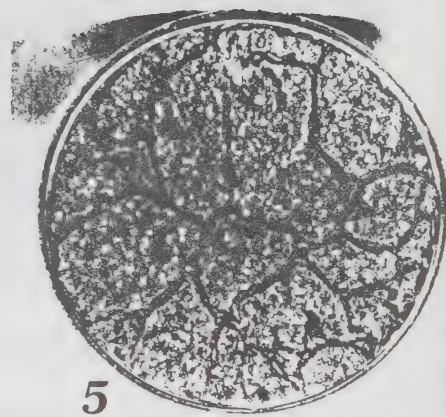


Fig. 35 - Gallery buildings of *Microcerotermes championi* at 100 (1), 200 (2), 300 (3, 4), 350 (5) and 400 % (6) water content of vermiculite after 4 weeks (bottom view) (Photo 4, 5 and 6 at page 132).



slowly. But between 300 and 400 % water content the feeding quantity curve was descended strongly.

All groups were dead within 10 - 12 weeks at 400 % water content of the vermiculite and in 13 - 15 weeks at 100 %. After 16 weeks the maximum number of surviving insects was 28 % at 300 % water content. Above and below 300 % water content the number of surviving insects was reduced.

As shown in Fig. 35 gallery building was more distinct at 200 to 300 % water content of the vermiculite.

From these results it is evident that 200 to 300 % water content is optimum for testing and culturing of *M. championi*.

3.2.1.7. *Nasutitermes nigriceps* (Haldeman)

Test period 1 - 4 weeks

During this period the wood consumption (Fig. 36) was slightly increased at higher stages of water content of the humus soil. At 26 to 38 % water content of the substrate the mortality of the insects was about similar but at 42 % it was a little less.

Test period 1 - 12 weeks

In 1 - 12 weeks there was a gradual increase in the wood consumption with raising the water content of the soil from 26 to 42 %. The ratio between maximum (at 42 % water content) and minimum (at 26 % water content) quantity of wood consumption was 1.3 : 1.

The amount of wood consumption in 5 - 12 (1 - 12 minus 1 - 4 weeks) was more than in 1 to 4 weeks and the insects in 5 - 12 weeks consumed gradually higher quantities of wood from lower to higher stages of water content of the soil. The ratio between the highest amount of wood consumption at 42 % water content and the lowest at 26 % water content was 1.4 : 1 in 5 - 12 weeks.

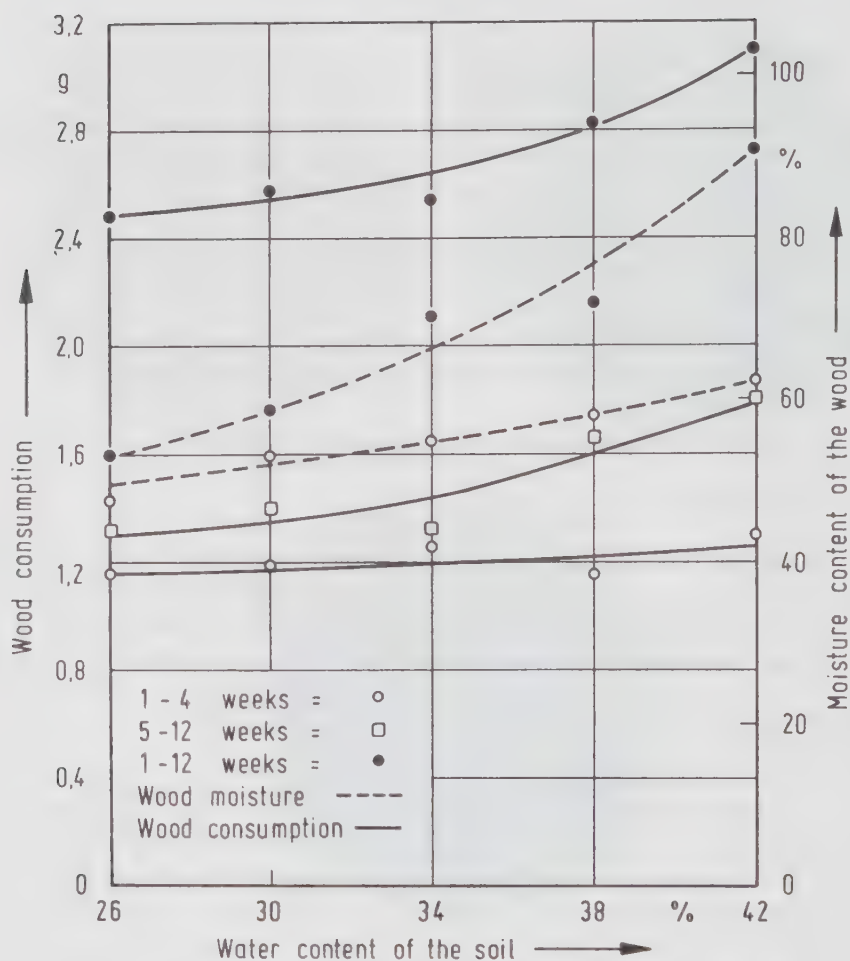


Fig. 36 - Wood consumption and wood moisture (birch wood) of *Nasutitermes nigriceps* in relation to water content of humus soil at 30°C and 98 to 99 % relative humidity of the room after different test periods (average of 4 replications).

Mortality of whole groups at different stages of water content of the soil occurred after following weeks. At 26 % water content 2 groups were dead after 4 weeks and the rest - 2 groups - within 10 to 11 weeks. At 30 % water content the first two groups were dead after 3 weeks, the third after 4 weeks and the fourth or last group survived up to 8 weeks. At 34 % water content the first group died after 4 weeks and the rest - 3 groups were dead within 7 to 9 weeks. At 38 % water content two groups were dead within 6 to 7 weeks, the third group after 11 weeks but in the fourth or last group about 65 % (from weight) of the insects were surviving after 12 weeks. At 42 % water content the first group was dead after 8 weeks, the second after 11 weeks. But in the rest two groups, about 40 to 50 % insects were surviving after 12 weeks.

In general *N. nigriceps* showed higher mortality during the tests than other tested species. In all the tests soldiers survived somewhat longer than workers.

With raising the moisture content of the soil from 26 to 42 % the mortality of the insects was gradually reduced.

3.2.2. Comparison of the results

3.2.2.1. Wood consumption

The total amount of wood consumed by *K. flavicollis*, *Z. angusticollis*, *C. formosanus*, *R. flavipes*, *H. indicola* and *M. championi* in relation to the moisture content of the vermiculite after 16 weeks is compiled in Fig. 37. It is obvious from the curves of wood consumption that the moisture requirements of termites varied from species to species. Some species were independent from the effect of the moisture content of vermiculite between 50 and 400 %, others required the lower range, while the rest fed and survived best in the upper moisture range of the substrate.

The amount of wood deterioration caused by *K. flavicollis* was about the same at all stages of the moisture content of vermiculite (Between 50 and 400 %). Therefore, 50 to 400 % moisture did not have any effect on the wood consumption of *K. flavicollis* (dry-wood termite). *Z. angusticollis* (Damp-wood termite) consumed slightly more wood at lower than at higher moisture contents of the vermiculite. At 400 % moisture the amount of wood deterioration was about 89 % of the optimum moisture conditions (200 %).

M. championi preferred a lower moisture content. It was very sensitive to higher moisture content of the substrate. At 200 % moisture it deteriorated the maximum amount of wood.

Fig. 37 - Total amount of wood consumption of *Kaloterмес flavicollis*, *Zootermopsis angusticollis*, *Heterotermes indicola*, *Coptotermes formosanus*, *Reticulitermes flavipes* and *Microcero-termes championi* in relation to the moisture content of the vermiculite after 16 weeks.

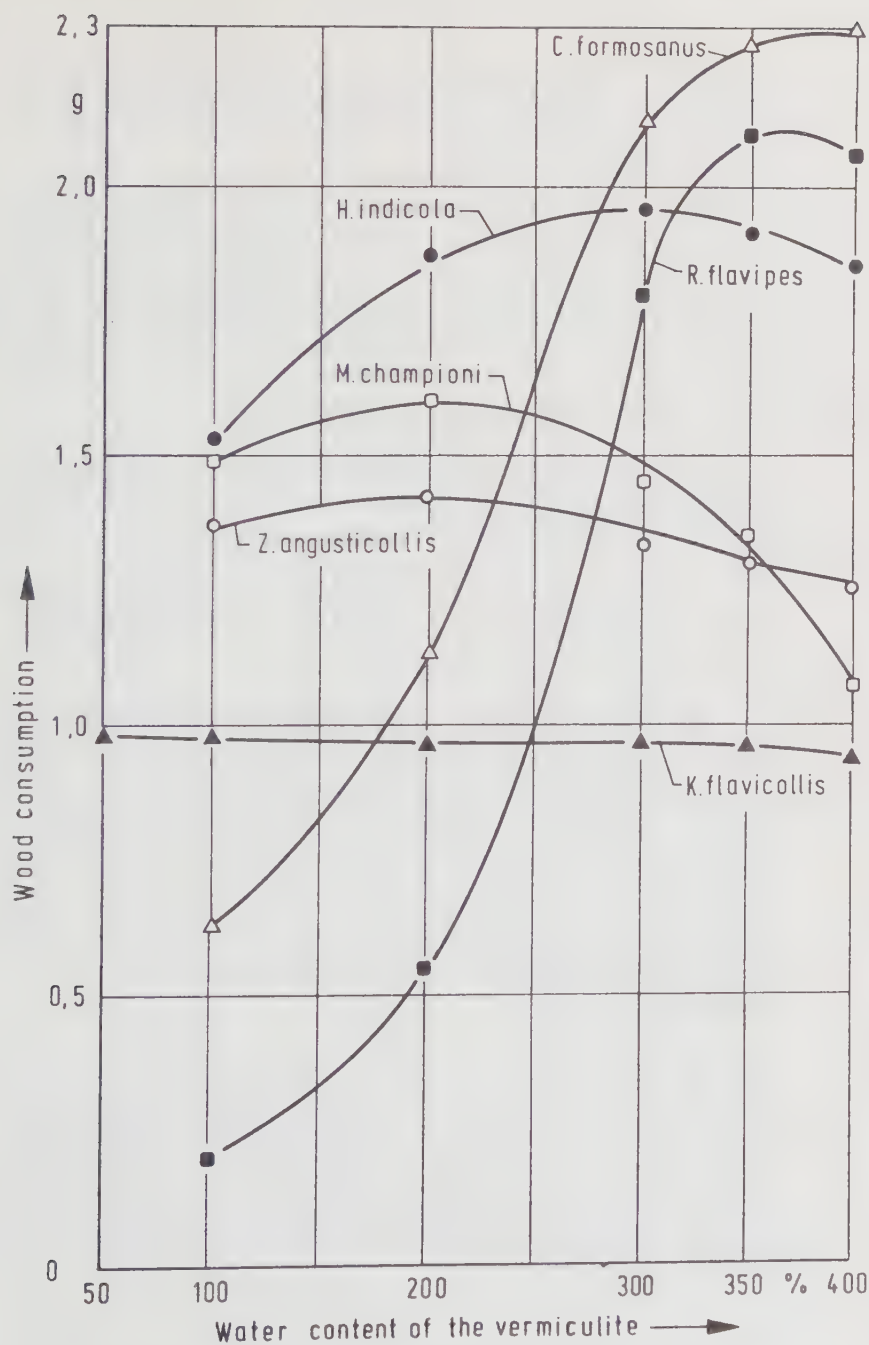


Fig. 37

The amount of wood consumption at the highest moisture (400 %) was about 70 % of that of the optimum moisture (200 %) content of the substrate.

H. indicola preferred a higher moisture but it can also tolerate lower moisture content of the substrate. 300 to 350 % moisture content of vermiculite was optimum for this termite. At 200 and 400 % moisture it consumed about the same amount of wood. At adverse (100 %) moisture content the amount of wood degradation was about 78 % of that of the optimum moisture (300 to 350 %) content of the vermiculite.

100 to 300 % water content of the substrate showed a very strong effect on wood consumption by *C. formosanus*. From 300 to 350 % moisture wood deterioration was increased slightly. However, at 350 and 400 % moisture wood consumption was about similar. At 100 % moisture the amount of wood deterioration was about 29 to 30 % of that of the optimum water content (350 to 400 %) of the substrate.

From 100 to 350 % moisture, there was a very strong increasing effect on wood consumption by *R. flavipes* but at 400 % moisture the feeding quantity was somewhat decreased. At 100 % moisture the amount of wood degradation was about 10 % of that of the optimum moisture (350 to 400 %) content of the vermiculite. *C. formosanus* and *R. flavipes* from Hamburg required a high moisture content of the substrate and both species were very sensitive to lower moisture content of the substrate.

With the increase of the moisture content of humus soil from 26 to 42 % the amount of wood consumption was increased slowly by *N. nigriceps*. The minimum amount of wood consumption at 26 % moisture was about 80 % of the maximum amount of wood deterioration at 42 % moisture. *N. nigriceps* required a higher moisture content of the soil but it was also tolerant to lower moisture content of soil.

Table 26

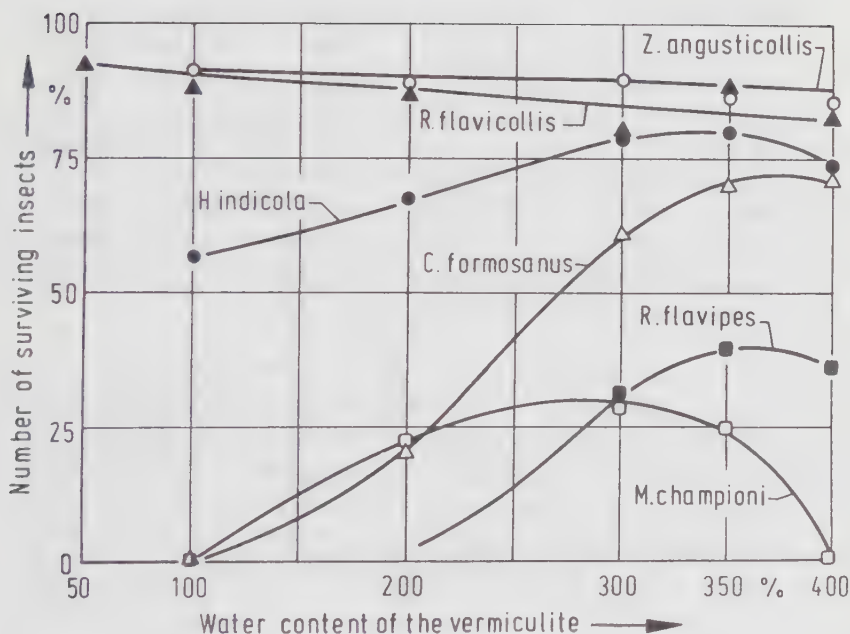
Amount of wood consumption per 100 mg insects (calculated from starting weight) in the optimum range of moisture content of the vermiculite after 8 weeks in the case of *Heterotermes indicola*, *Kalotermes flavicollis*, *Reticulitermes flavipes*, *Coptotermes formosanus*, *Zootermopsis angusticollis* and *Microcerotermes championi*.

Species of termites	Amount of wood consumption (mg)	Optimum range of moisture content of vermiculite (%)
<i>H. indicola</i>	177 - 178	300 - 350
<i>K. flavicollis</i>	168 - 171	50 - 400
<i>R. flavipes</i>	167 - 168	350 - 400
<i>C. formosanus</i>	140 - 144	350 - 400
<i>Z. angusticollis</i>	120 - 122	150 - 250
<i>M. championi</i>	68 - 70	200 - 300

H. indicola showed the highest amount (Table 26) of wood consumption which was followed by *K. flavicollis* and *R. flavipes*. *K. flavicollis* and *R. flavipes* deteriorated about the same amount. *C. formosanus* and *Z. angusticollis* followed the above species respectively. The amount of wood consumption by *M. championi* was the lowest of all the species of termites. Although *R. flavipes* showed a high mortality during the experiment, this termite degraded a high amount of wood. These studies confirmed that *H. indicola*, *K. flavicollis* and *R. flavipes* were the most suitable species for laboratory tests. *M. championi* and *N. nigriceps* were the least suitable species for tests. These results are in agreement with the results of G. Becker and D. Puchelt (1961), G. Schultze-De-witz (1961), G. Becker (1962c, 1965a, 1970a), G. Becker and M. Lenz (1970) and G. Becker, M. Lenz and M. Garcia (1976).

3.2.2.2. Survival

The number of the surviving insects (Fig. 38) of the species *Z. angusticollis* was about the same at all the stages of moisture content (100 to 400 %) of the vermiculite. But *K. flavicollis* showed a slight decrease in the survival of insects with increasing moisture content of the vermiculite (50 to 400 %). Both species showed the lowest mortality rate at all the stages of water contents of the vermiculite. *C. formosanus* and *R. flavipes* preferred a high moisture content of the substrate and showed the highest mortality at 100 % moisture content of the substrate. During the tests, *R. flavipes* showed a higher mortality than *C. formosanus*. *H. indicola* also preferred higher moisture but was able to tolerate lower moisture conditions too. It showed a higher mortality than *Z. angusticollis* and *K. flavicollis* and less mortality than the rest of the termite species. *M. championi* showed the highest mortality at lowest (100 %) and highest (400 %) moisture content of the vermiculite. The maximum survival of insects was 28 % at 300 % moisture. Nevertheless, this termite



Tab. 38 - Number of surviving insects (%) of *Kalotermes flavicollis*, *Zootermopsis angusticollis*, *Heterotermes indicola*, *Coptotermes formosanus*, *Reticulitermes flavipes* and *Microcerotermes championi* in relation to the water content of the vermiculite after 16 weeks.

revealed the highest mortality rate of all the species. These results agree with G. Becker and D. Puchelt (1961), G. Schultze-Dewitz (1961), G. Becker (1962c, 1965a, 1970a), I. Hrdy and J. Zeleny (1967) and G. Becker and M. Lenz (1970).

3.2.2.3. Wood moisture

As shown in Table 27, between 100 and 200 % moisture content of the vermiculite, the wood moisture rose slowly and from 200 to 300 % water content of the substrate, the wood moisture rose more rapidly. There was a very strong increase in the wood moisture from 300 to 400 % moisture content of the vermiculite.

The absorption of water by the wood was effected by the species of termites. The wood pieces which were excavated by the insects showed a higher moisture content (*K. flavicollis*, *H. indicola*, *R. flavipes* and *C. formosanus*). The moisture content of the wood was relatively low in the case of *Z. angusticollis* and *M. championi* which fed only on the surface of the wood pieces. (G. Becker, 1965a, 1970a and G. Becker and M. Lenz, 1970).

Table 27

Percentage of wood moisture (average from 1 - 4, 5 - 8 and 9 - 16 weeks) in relation to the moisture content of the vermiculite in the case of *Kaloterms flavicollis*, *Heterotermes indicola*, *Coptotermes formosanus*, *Reticulitermes flavipes*, *Zootermopsis angusticollis* and *Microcerotermes championi*.

Species of termites	Wood moisture (%) in relation to moisture content of the vermiculite				
	100	200	300	350	400
<i>K. flavicollis</i>	35	39	50	99	184
<i>Z. angusticollis</i>	34	34	44	75	123
<i>H. indicola</i>	35	39	52	72	158
<i>C. formosanus</i>	36	44	61	147	162
<i>R. flavipes</i>	32	39	55	122	138
<i>M. championi</i>	41	43	68	114	121

4. DISCUSSION

These investigations have shown that the reaction of termites to the relative humidity of the air, under starvation conditions is different from species to species.

All the species of Termopsidae, Rhinotermitidae and Termitidae which were tested survived best at a high (100 %) relative humidity of the air and proved to be very susceptible to low atmospheric moisture. Therefore, they are typically stenohygrous insects. This behaviour of these species is due to their natural living conditions. The authors cited in the introduction investigated the desiccation resistance of some species of the families Termopsidae, Rhinotermitidae and Termitidae. They also observed that these insects prefer a high atmospheric moisture.

The 3 species of Kalotermitidae, i.e. *Neotermes jouteli* (Banks), *Kalotermes flavicollis* (Fabricius) and *Cryptotermes dudleyi* Banks revealed a higher resistance to desiccation than Termopsidae, Rhinotermitidae and Termitidae species. Optimum conditions of relative humidity for the survival of these 3 species of dry-wood termites are below 100 %. G. Becker (1969) and M. S. Collins (1969) also stated that Kalotermitidae are more resistant to desiccation than Termopsidae, Rhinotermitidae and Termitidae species. Kalotermitidae species were tested by several authors quoted in the introduction. They all came to similar results regarding the behaviour of these insects against dryness.

Our tests also showed that *Cryptotermes dudleyi* withstand low atmospheric moisture better than *Kalotermes flavicollis* and *Neotermes jouteli*. These results coincide with the natural conditions in which these insects are used to live. *Cryptotermes dudleyi* lives under dry conditions (furniture, constructional timber in houses etc.) whereas, in nature *Neotermes jouteli* prefers relatively damp wood and *Kalotermes flavicollis* in nature occupies the intermediate position. A. G.

Richards and M. S. Collins (1966) tested 8 species of dry-wood termites for their resistance to desiccation and they found *Cryptotermes brevis* (Walker) to be the most resistant one. Similarly, M. S. Collins (1969) observed that *Neotermes* and *Kaloterme*s species live for shorter periods under desiccation than *Incisitermes*, *Marginitermes*, *Pterotermes* and *Cryptotermes* species. G. Becker (1969) also stated that *Cryptotermes* require less moisture than *Kaloterme*s and *Neotermes* species. *Neotermes* require 98 % relative humidity, but *Bifiditermes beesoni* (Gardner) and *Cryptotermes bengalensis* (Snyder) survived best at 92 % relative humidity (P. K. Sen-Sarma, 1974). D. R. Minnick, S. H. Kerr and R. C. Wilkinson (1973) also found that *Cryptotermes brevis* (Walker) survived best at 87 % relative humidity. R. M. C. Williams (1976, 1977) also revealed that *Cryptotermes* species are very resistant against dry conditions.

Kalotermitidae species exposed to higher atmospheric moisture, became floated and died quickly. A similar reaction has been found with *Cryptotermes brevis* (M. S. Collins, 1969, D. R. Minnick, S. H. Kerr and R. C. Wilkinson, 1973). The early death of dry-wood termites at higher atmospheric moisture may be due to water poisoning, stated first by P. A. Buxton in 1932. According to E. Bursell (1964) this effect occurs when metabolic water is produced in quantities that cannot be eliminated by evaporation and the water content rises above the normal level in the body. It is also assumed that at higher atmospheric moisture the insects were attacked by fungi.

Zootermopsis angusticollis (Termopsidae) is more resistant to desiccation than *Rhinotermitidae* and *Termitidae* species. This has also been investigated by R. Geigy and E. Ernst (1951), E. Ernst (1956) and M. S. Collins (1969) with *Zootermopsis nevadensis*.

Heterotermes indicola (Wasmann), *Prorhinotermes simplex* (Hagen), *Microcerotermes championi* Snyder, *Microcerotermes crassus* Snyder and *Nasutitermes nigriceps* (Haldeman) which are found

in tropical parts of the world, were resistant to desiccation. But they revealed a higher susceptibility against dryness than dry-wood termites (*Neotermes*, *Kalotermes* and *Cryptotermes*) and damp-wood termites (*Zootermopsis*). *Heterotermes indicola* was most resistant to dryness of all the *Rhinotermitidae* and *Termitidae* species. M. S. Collins (1969) also observed that *Heterotermes aureus* (Snyder) is more resistant than *Reticulitermes* species.

These investigations have shown that *Heterotermes indicola* from 30°C culture are slightly more resistant to dryness in comparison to animals from 26°C culture. G. Becker (1970a) received similar results with *Reticulitermes* species.

Coptotermes formosanus (Shiraki) (*Rhinotermitidae*) is distributed on the coastal areas of tropical and subtropical parts of the world. This termite is adapted to higher moisture conditions. Our studies have also shown that *Coptotermes formosanus* is very sensitive to low atmospheric humidity. But at higher relative humidity (100 %) it survived about as long as *Prorhinotermes simplex* and *Nasutitermes nigricipes*.

It is surprising that the tropical termite *Coptotermes niger* Snyder is most susceptible to desiccation of all the species of termites tested. The reason for this unexpected reaction of the species is not known.

Apart from *Heterotermes indicola*, *Reticulitermes tibialis* Banks revealed the highest resistance to dryness of all the species of *Rhinotermitidae* and *Termitidae*. Moreover, *Reticulitermes tibialis* survived longest under desiccation conditions of all the species of the genus *Reticulitermes*. A high resistance of *R. tibialis* against dry conditions has also been revealed by other authors cited in the introduction. The geographical distribution of *Reticulitermes tibialis* in arid parts of North and Central America also proved that this termite is resistant to dryness (C. A. Kofoid, 1934, M. J. Strickland, 1950, T. E. Snyder, 1954, F. M. Weesner, 1965 and M. S. Collins, 1969).

Reticulitermes hesperus the culture of which originated from the southern part of the USA (Los Angeles) is less resistant than *Reticulitermes tibialis*. It was also reported by many authors. But it was more resistant to dryness than the other *Reticulitermes* species tested. *Reticulitermes flavipes*, *Reticulitermes lucifugus*, *Reticulitermes santonensis*, *Reticulitermes virginicus*, *Reticulitermes speratus kyushuensis* and *Reticulitermes speratus speratus*, which are found mainly in temperate climate, such as South Europe, North America and Northern East Asia, proved to be sensitive to desiccation. The tested *Reticulitermes* species from temperate climate showed only slight differences in desiccation resistance. *Reticulitermes santonensis* proved to be the most resistant one. This result was also obtained by G. Becker (1970a) who tested temperature and moisture requirements of several *Reticulitermes* species.

There were differences in the desiccation resistance of animals from different geographical origin but of the same species (*Reticulitermes flavipes* from Hamburg, Hallein and Charleston (USA) and *Reticulitermes lucifugus* from Favone, Francavilla and Munich). This was also observed by G. Becker (1970a) with *Reticulitermes flavipes* and by G. Rascia (1961) with *Reticulitermes lucifugus*.

In these tests the differences in the desiccation resistance of sub-species were also observed, e.g. *Reticulitermes speratus kyushuensis* (from Korea) survived longer under starvation conditions than *Reticulitermes speratus speratus* (from Japan).

Differences in the behaviour of the castes of termites against desiccation were also observed by other authors. Workers are more resistant against desiccation than soldiers, which was also observed by G. Becker (1942), M. J. Strickland (1950), R. Geigy and E. Ernst (1956) and P. K. Sen-Sarma (1969). In heterogeneous groups (workers and soldiers together) soldiers are fed by workers. This has an effect on the survival period of both castes. In comparison to homogenous groups, survival of

soldiers was increased and survival of workers decreased. Furthermore, in heterogenous groups (*Coptotermes niger*, *Reticulitermes flavipes* from Charleston and *Nasutitermes nigriceps*) soldiers lived somewhat longer than workers in contrast to the results with homogenous groups. Only *Coptotermes formosanus* in heterogenous groups showed that workers are more resistant against drying than soldiers. The reason for this behaviour of *Coptotermes formosanus* is unknown. Finally, it can be said that starvation has an important effect on the resistance against desiccation of soldiers in most of the species of termites.

Our studies have also confirmed that isolated animals are more susceptible to desiccation than grouped ones. This has also been stated by other authors quoted in the introduction.

According to P. P. Grassé and R. Chauvin (1944) an increase in the survival period of grouped insects is due to sensory stimuli among the grouped animals. R. J. Pence (1956) suggested that clustering behaviour or "huddling" occurs in grouped insects. This blustering behaviour causes a reduction of the exposed surface, which results in an increase in the survival of grouped animals.

According to E. Ernst (1956), J. Alibert (1959), P. K. Sen-Sarma and W. Kloft (1965), P. K. Sen-Sarma (1965, 1969) and G. Becker (1969) trophallactic exchange among the grouped workers is the main factor for the increase in the survival period.

Our tests have also shown that grouped workers are more resistant to desiccation compared with isolated workers than grouped soldiers compared with isolated soldiers. From these results, it is evident that trophallactic exchange between workers is an important factor for increasing the survival period. In the case of soldiers which cannot feed themselves, sensory stimuli and clustering behaviour appear to be responsible for the longer survival period of grouped animals.

The lack of trophallactic exchange, responsible for the higher mortality rate of homogenous soldier groups is clearly shown in comparison with the results of heterogenous groups. These soldiers (in heterogenous groups) lived longer because they were fed by workers.

It is also assumed that the evaporation of grouped animals is more than that of isolated ones. This may result to the increase of moisture content of the air in the container. It may be one of the causes effecting the increasing longevity of the grouped animals.

Investigations with four species of the genus *Reticulitermes* have shown that nymphs are more resistant to desiccation than workers. M. J. Strickland (1950), L. G. Dunmore and M. S. Collins (1951), M. S. Collins and A. G. Richards (1963) and M. S. Collins (1969) also explained that nymphs withstand desiccation better than workers.

Differences in the susceptibility of grouped and isolated animals varied according to the size of the natural colony, e.g. *Nasutitermes nigriceps* and *Microcerotermes crassus* (Termitidae) revealed the highest difference in the survival period of grouped and isolated animals and these species have the largest size of natural colonies. Similarly, *Coptotermes formosanus* (Rhinoitermitidae) with middle-sized colonies showed intermediate difference in the longevity of grouped and isolated insects. *Reticulitermes* species (Rhinoitermitidae) which have the smallest size of natural colonies in comparison to above mentioned species, showed lowest differences in the susceptibility of grouped and isolated animals. The 4 different species of the genus *Reticulitermes* which have about the same size of natural colonies showed about the same difference in the survival period of grouped and isolated individuals. These results coincide with G. Becker (1969) that the smaller the natural colonies are, the lower may be the number of animals in the test groups.

It has been determined that the reaction of termites against different stages of the water content of substrate varied from species to species. From 50 to 400 % the water content of the vermiculite has no effect on the wood consumption of *Kaloterms flavicollis*. R. J. Pence (1956) stated that *Kaloterms nimor* Hagen sealed in a desiccated wood showed the same reaction, either the infested wood was kept in a desiccator or at ordinary room conditions. In wood choice tests (G. Becker, 1965a) with wood pieces of different moisture content, *Kaloterms flavicollis* preferred lower wood moisture (20 - 30 %). G. Hrdy and J. Zeleny (1967) revealed that *Kaloterms jouteli* Banks prefers dryer wood too. The higher resistance of *Kaloterms flavicollis* (dry-wood termite) against dryness has been stated by many authors. In nature this termite is mostly found in dry, dead branches of trees, dry logs, litters of wooden areas and in the buildings usually without any contact to the soil. But destruction of living trees and plants by this termite is also not impossible. So, *Kaloterms flavicollis* is not only found in dry atmospheric environments. Field and laboratory observations have shown that this termite prefers higher atmospheric moisture too. Nevertheless, under a choice test, this termite prefers dry wood, but during compulsory feeding it destroys moist wood also in the same amount. This ability of *Kaloterms flavicollis* to adapt itself to extremes of humidity and aridity makes it a successful species under all conditions.

These studies showed that *Zootermopsis angusticollis* (damp-wood termite) consumed slightly larger wood at 200 % water content than at higher percentage of water content of the vermiculite. During wood choice test with different water contents of wood pieces and with compulsory feeding tests at different water content of the soil, *Zootermopsis nevadensis* (Hagen) preferred moist wood (G. Becker, 1965a). In nature *Zootermopsis* species are found in moist rain forest on the west coast of North America. In buildings, this termite is also found in moist wood. It has also been found that the spe-

cies *Zootermopsis angusticollis* is dominant in coastal areas. Therefore, it is quite reasonable to call it a damp-wood termite.

Heterotermes indicola, *Coptotermes formosanus* and *Reticulitermes flavipes* required a higher moisture content of the substrate. *Heterotermes indicola* can tolerate to some extent low moisture content of soil whereas, *Reticulitermes flavipes* and *Coptotermes formosanus* showed a very high susceptibility to lower moisture content of the substrate. Moisture requirement of *Coptotermes formosanus* was slightly higher than that of *Reticulitermes flavipes* and *Heterotermes indicola* (G. Becker and D. Puchelt, 1961, G. Becker, 1962, 1965a, 1970a and G. Becker and M. Lenz, 1970).

G. Becker and M. Lenz (1970) showed that *Coptotermes amanii* Sjöstedt required lower moisture content of the substrate than *Reticulitermes*, *Heterotermes* and *Nasutitermes* species. But our investigations have shown that *Coptotermes formosanus* required higher moisture contents of soil than *Coptotermes amanii*. This can be explained by comparison of the geographical distributions of these two species. *Coptotermes amanii* originated from Mombasa (Kenya) (tropical conditions) and *Coptotermes formosanus* originated from a different climate, Lake Charles, La. USA.

Microcerotermes championi which is found in the tropical parts of the Indian sub-continent preferred 200 to 300 % water content of the substrate. It shows great sensitiveness to higher moisture. Similar observations were made by P. K. Sen-Sarma and P. N. Chatterjee (1968) with *Microcerotermes beelsoni* Snyder and by I. Hrdy (1970) with *Microcerotermes cameroni* Snyder.

Nasutitermes nigriceps showed a slow increase in the amount of wood consumption with the increase of moisture content of the humus soil. This species required a high moisture content of the substrate, but showed tolerance to lower moisture content too (G. Becker and M. Lenz, 1970).

Inspite of higher mortality *Reticulitermes flavipes* proved a very destructive species whereas, *Zootermopsis angusticollis* with a very low mortality showed only a low amount of wood consumption. Similar correlations between mortality and wood destructions were described by G. Schultze-Dewitz (1961), G. Becker (1962c, 1970a) and G. Becker and M. Lenz (1970).

Gallery building activities inside the substrate proved to be usual for *Rhinotermitidae* species. In other termite species only *Microcerotermes championi* showed such activities. *Heterotermes indicola* revealed strongest gallery building (inside and outside the substrate) qualities of all the tested species (Becker, 1962c, 1965a, 1972a).

Wood deterioration depends on the water content of the substrate and is not effected by moisture contents of the wood (at least above the fiber saturation of the wood). In these tests wood moisture between 32 to 184 % proved to be not effective on wood deterioration. G. Becker (1965a, 1970a) and G. Becker and M. Lenz (1970) also got similar results.

The effect of humidity and nutrition on caste development by *Rhinotermitidae* species was studied by G. Becker and M. Lenz (1970). The results with *Reticulitermes* and *Heterotermes* species coincide with the results reported in this paper.

There was no development in tests with *Coptotermes*, *Microcerotermes* and *Nasutitermes* species. F. J. Gay et al. (1955), G. Becker (1966c) and I. Hrdy (1966) revealed that *Coptotermes* species seldom or never produce neotenic reproductives.

From these investigations on the development of termites, it is suggested that long period tests with high number of individuals may be more successful for further experiments.

5. SUMMARY

Comparative investigations on the survival period of various species, sub-species and castes of termites have been carried out under starvation conditions in relation to relative humidity of the air. For these tests, the insects were exposed at 33, 63, 75, 85, 93, 98 and 100 % relative humidity. The investigated species were *Neotermes jouteli*, *Kaloterms flavicollis*, *Cryptotermes dudleyi* (Kalotermitidae), *Zootermopsis angusticollis* (Termopsidae), *Heterotermes indicola*, *Coptotermes formosanus*, *Coptotermes niger*, *Reticulitermes flavipes* (from Hamburg, Hallein and Charleston), *Reticulitermes hesperus*, *Reticulitermes lucifugus* (from Favone, Francavilla and Munich), *Reticulitermes santonensis*, *Reticulitermes speratus kyushuensis*, *Reticulitermes speratus speratus*, *Reticulitermes tibialis*, *Reticulitermes virginicus*, *Prorhinotermes simplex* (Rhinotermitidae), *Microcerotermes championi*, *Microcerotermes crassus* and *Nasutitermes nigriceps* (Termitidae). All the tests were carried out at 26°C except those with *Zootermopsis angusticollis* which was investigated at 20°C. The survival period was calculated in days.

The survival period under different percentages of relative humidity differs not only in different species and sub-species but even in the same species it varies from caste to caste.

The Kalotermitidae species proved to be more resistant to dryness than Termopsidae, Rhinotermitidae and Termitidae species. Dry-wood termites (Kalotermitidae) were less susceptible to dry environmental conditions. The optimum range of relative humidity under starvation conditions was 90 to 99 % for *Neotermes jouteli*, 80 to 95 % for *Kaloterms flavicollis* and *Cryptotermes dudleyi* survived best between 33 and 85 % relative humidity. Resistance against desiccation decreased from *Cryptotermes dudleyi*, *Kaloterms flavicollis* and *Neotermes jouteli*. *Cryptotermes dudleyi* was most resistant of all the tested species.

100 % relative humidity proved to be optimum for Termopsidae, Rhinotermitidae and Termitidae species.

The Termopsidae species revealed a higher resistance to desiccation than Rhinotermitidae and Termitidae species.

The Rhinotermitidae and Termitidae species were very sensitive to dry environmental conditions and at low atmospheric moisture they showed less differences in the survival period.

Heterotermes indicola and *Reticulitermes tibialis* proved to be the most resistant of all Rhinotermitidae and Termitidae species.

Coptotermes niger and *Reticulitermes speratus speratus* proved to be the most susceptible of all the species of termites tested.

Animals from different geographical origin but of the same species showed differences in the desiccation resistance.

A species from the same geographical origin but cultured at different temperatures revealed different reactions against desiccation.

Workers showed a higher resistance to desiccation than soldiers, whereas, in heterogenous groups soldiers survived longer (except *Coptotermes formosanus*) than workers.

Nymphs withstand desiccation conditions better than workers.

Grouped animals survived longer than isolated individuals.

The difference in the survival time of grouped and isolated workers was higher than the difference between the survival periods of grouped and isolated soldiers.

The difference in the longevity of grouped and isolated individuals was greater in termite species of large-sized natural colonies than those species which have comparatively smaller sizes of natural colonies.

The survival time of various species and castes of termites under desiccation and starvation conditions was not dependent on the body weight of the insects.

No cannibalism was observed in case of the *Microcerotermes* and *Nasutitermes* (Termitidae) species.

The influence of different stages of moisture content of the substrate on the wood consumption, mortality, gallery building and development of various species have been determined.

Kaloterme flavicollis (Kalotermitidae), *Zootermopsis angusticollis* (Termopsidae), *Heterotermes indicola*, *Coptotermes formosanus*, *Reticulitermes flavipes* from Hamburg (Rhinotermitidae) and *Microcerotermes championi* (Termitidae) species were tested with vermiculite. But *Nasutitermes nigriceps* was studied with humus soil.

Kaloterme flavicollis fed about the same amount of wood at all the stages of moisture content (50 to 400 %) of vermiculite. The optimum moisture content of vermiculite was 150 to 250 % for *Zootermopsis angusticollis*, 300 to 350 % for *Heterotermes indicola*, 350 to 400 % for *Reticulitermes flavipes* from Hamburg and for *Coptotermes formosanus* and 200 to 300 % for *Microcerotermes championi*. *Nasutitermes nigriceps* deteriorated the maximum quantity of wood at 42 % moisture content of the humus soil. Wood consumption is dependent on the water content of the substrate but not on the moisture content of the wood.

Heterotermes indicola, *Kaloterme flavicollis* and *Reticulitermes flavipes* from Hamburg proved to be the most destructive of all the tested species. *Microcerotermes championi* and *Nasutitermes nigriceps* deteriorated the lowest amount of wood of all the investigated species.

Zootermopsis angusticollis, *Kaloterme flavicollis* and *Heterotermes indicola* revealed the lowest but *Nasutitermes nigriceps* and *Microcerotermes championi* showed the highest mortality rate during the investigations.

The absorption of water inside the wood pieces is effected by the termites species due to their mode of feeding (feeding on the surface or inside the wood pieces).

Excavation inside the wood pieces was strongest by *Kaloterme flavicollis*.

The effect of the moisture content of the substrate on the development of termites varied from species to species. The development of different castes of the same species was also depending on different stages of moisture content of the substrate.

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Autobiography

On May 2nd., 1948, I was born in 277/R. B. Lyall Pur, Pakistan to Fazal Khan, farmer and Rashida Begum, housewife. I have an elder sister and a younger brother. My parents migrated from East Punjab (India) to West Punjab (Pakistan) during the independence and partition of India in August, 1947.

I attended my village primary school from 1953 to 1958 and from 1958 to 1963, D. C. high school Pacca Anna. From 1963 to 1965, I attended the Government college Gojra. In 1966, I began studies at the Government college Lyall Pur and in 1968, I received the degree "Bachelor of Science" from the Punjab university Lahore. From 1968 to 1970, I joined the Government college Lahore and I received the degree "Master of Science". from the Punjab university Lahore in 1970. From 1971 to 1972, I worked voluntarily as a lecturer of Biology in some intermediate colleges in Pakistan.

From summer semester 1973 to summer semester 1974, I joined the Technische Universität Berlin, where, in July 1974, I passed the German language examination. From winter semester 1974/75 to the end of 1975, I studied Biology at the Freie Universität Berlin. In January 1976, I began my Ph. D. research at the Bundesanstalt für Materialprüfung Berlin-Dahlem.

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